



**HAL**  
open science

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

Émile Brisson-Curadeau, Charles-andré Bost, Yves Cherel, Kyle Elliot

## ► To cite this version:

Émile Brisson-Curadeau, Charles-andré Bost, Yves Cherel, Kyle Elliot. King penguins adjust foraging effort rather than diet when faced with poor foraging conditions. *Ibis*, 2024, 166, pp.723-731. <10.1111/ibi.13287>. <hal-04284040>

**HAL Id: hal-04284040**

**<https://hal.science/hal-04284040v1>**

Submitted on 14 Nov 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

1 **King penguins adjust foraging effort rather than diet when faced with poor foraging conditions**

2 Émile Brisson-Curadeau<sup>1,2\*</sup>, Charles-André Bost<sup>1</sup>, Yves Cherel<sup>1</sup>, Kyle Elliott<sup>2</sup>,

3

4 \* Corresponding author

5 1 : Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 du CNRS-La Rochelle Université, Villiers-en-

6 Bois, France

7 2 : Natural Resource Sciences, McGill University, Quebec, Sainte-Anne-de-Bellevue, Canada

8

9

10

11

12 keywords: diet, Southern Ocean, specialist, isotope, foraging, seabird, king penguin

13

14

15

16 **Abstract**

17

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

26 **Intro**

27 There are multiple strategies available to birds to cope with periods of low prey availability. For example,  
28 dietary-specialist species can increase foraging effort to compensate for low prey capture rates (Abrams  
29 1991, Cox et al. 2019, Fromant et al. 2021). Alternatively, generalists can switch to feeding on other still-  
30 available prey (Scopel et al. 2019, Milchev & Georgiev 2020). The strategy chosen is highly species-  
31 dependant, with both specialist and generalist displaying variable flexibility in both foraging effort and  
32 diet.

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

43 Here, we investigate the links between foraging success, foraging effort, and diet in a specialist deep-diving  
44 seabird, the King Penguin *Aptenodytes patagonicus*. This species feeds mainly on small mesopelagic  
45 myctophids, often dominated by *Krefftichthys anderssoni*, for which the availability to the top predators  
46 may change across the polar region, mainly due to climatic anomalies (Bost et al. 2002, Bost et al. 2015,  
47 Le Bohec et al. 2008, Péron et al. 2012). Yet, King Penguins can also forage opportunistically on other prey

48 such as squids and other myctophids (Adams & Klages 1997, Bost et al. 2002, Cherel et al. 2007).  
49 Consequently, the species could theoretically diversify its diet in periods of low prey availability.

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

57

## 58 **Methods**

59 All data were collected in February on chick-rearing King Penguins at Ratmanoff's colony (around 85 000  
60 pairs, Barbraud et al. 2020) in the Kerguelen archipelago (-49° 14' 33", 70° 33' 40") situated in the southern  
61 Indian Ocean. Data were obtained during the chick-rearing period in all years from 2015 to 2022 except  
62 2019 (i.e. seven years total). The ethics committee of the Institut polaire français Paul-Émile Victor  
63 approved all field procedures.

64 King penguins of this colony feed mostly on a small myctophid, *Krefflichthys anderssoni*, and  
65 opportunistically (up to 25% of their diet) on other prey such as other fish species and squids (Bost et al.  
66 2002, Cherel et al. 2010, Cherel et al. 2011). During the chick-rearing period, parents make trips at sea  
67 lasting about 4 to 10 days. While prey availability estimates are not known during the study period, the  
68 years 2015 and 2016 were possibly less favorable for King Penguins at Kerguelen (Brisson-Curadeau et al.  
69 2023).

70

71 *Isotopic analysis*

72 Stable isotopes of nitrogen ( $\delta^{15}\text{N}$ ) are considered to be indicative to the trophic position of consumers,  
73 thus reflecting its diet, while  $\delta^{13}\text{C}$  is a proxy of the consumers' foraging habitat (Hobson et al. 1994,  
74 Quillfeldt et al. 2005, Cherel & Hobson 2007). The resulting isotopic niche described by these two isotopes  
75 can be thus used as a proxy of the consumers' trophic niche.

76 Since 2015, 83 chick-rearing penguins were blood sampled (2 ml) after their return from a single foraging  
77 trip. Birds were captured using a long wooden perch. The blood was freeze-dried and about 0.7mg was  
78 weighed into tin capsules. The capsules were shipped for bulk stable isotopes ratio of nitrogen ( $^{15}\text{N}/^{14}\text{N}$ )  
79 and carbon ( $^{13}\text{C}/^{12}\text{C}$ ) at the Ján Veizer Stable Isotope Laboratory (Ottawa, Ontario, Canada). Isotopic  
80 composition was measured by combustion on an Elementar VarioEL Cube Elemental Analyser followed by  
81 "trap and purge" separation and on-line analysis by continuous-flow with a DeltaPlus Advantage isotope  
82 ratio mass spectrometer coupled with a ConFlo III interface. The isotope concentration determination used  
83 the following conventional equation:

84 
$$\delta = ([R_{\text{sample}}/R_{\text{standard}}]-1) * 1000$$

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

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

92

93 *Foraging effort*

94 Foraging effort during the foraging trip was determined using biologgers from various brands recording  
95 GPS location and/or depth. Some of these loggers also recorded 3D acceleration (starting in 2020) as well  
96 as water temperature. Over the seven years, 52 birds were equipped with one or two of these devices (see  
97 Table S2-S3 for exact sample size by year). Loggers were retrieved after a single foraging trip. Penguins  
98 were weighed before and after each foraging trip. The weigh of the loggers varied with models, but never  
99 exceeded 2% of the bird's mass.

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

107 Due to logistical reasons, not all blood sampled penguins were assessed for foraging effort. Reasons  
108 explaining this mismatch include logger failures and logger detachment.

109 *Conditions encountered and foraging success*

110 King Penguins target the depth just below the thermocline to capture prey (Charrassin & Bost 2001,  
111 Scheffer et al. 2016). Consequently, shallower thermoclines are more accessible and therefore provide  
112 better conditions for foraging penguins. To assess the conditions encountered, we therefore combined  
113 depth data and temperature data to calculate the depth of the thermocline for each dive. We defined the

114 thermocline as the depth where the change in temperature was the greatest (see Charrassin & Bost 2001).  
115 We then calculate the average thermocline depth among all dives for each individuals.  
116 We computed two metrics of foraging success. First, we calculated the mass gained per day of foraging at  
117 sea. A second metric was computed using the accelerometry data: the number of Prey Capture Attempts  
118 (PCAs) in each dive was estimated with the algorithm from Brisson-Curadeau et al. (2021) using the  
119 number of acceleration peaks in the dive. We then used the number of PCAs per day as a measure of  
120 foraging success.

121

## 122 *Statistics*

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

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

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

138 All analysis were conducted in R version 4.1. Package lme4 was used to build the mixed-effect models  
139 (Bates et al. 2015). Validation of assumptions were conducted on all models (see also table S4). We tested  
140 for heteroskedasticity of residuals using the Breusch Pagan test on the lmtest package (Breusch 1978,  
141 Zeileis & Horton 2002). Pearson correlation test were conducted between residuals and the independent  
142 variables, while the autocorrelation in the residuals was assessed by extracting the autocorrelation  
143 coefficient (Venables & Ripley 2002).

144

## 145 **Results**

### 146 *Foraging behavior*

147 Most foraging effort indices varied greatly among individuals (Fig. 1), as shown by the standard deviation  
148 ( $\sigma$ ) and mean ( $\mu$ ) of total vertical distance travelled ( $\mu = 123$  km,  $\sigma = 62$  km,  $n = 48$ ), trip duration ( $\mu = 8.5$   
149 days,  $\sigma = 3.1$  days,  $n = 53$ ) and mean distance from the colony ( $\mu = 251$  km,  $\sigma = 102$  km,  $n = 36$ ). To a lesser  
150 degree, mean diving depth also differed among individuals ( $\mu = 141$ m,  $\sigma = 16$  m,  $n = 48$ ). Two foraging  
151 success variables, mass gained per day ( $\mu = 0.28$  kg/day,  $\sigma = 0.15$  kg/day,  $n = 31$ ) and PCAs per day ( $\mu = 406$   
152 PCAs/day,  $\sigma = 185$  PCAs/day,  $n = 52$ ) also varied greatly from one individual to another. When testing for  
153 among-year differences, only mean depth and total vertical distance showed significance (Fig. 1, Table S5).

154

### 155 *Stable isotopes*

156 Model selections showed that blood  $\delta^{13}\text{C}$  ( $-22.0 \pm 0.4\text{‰}$ ,  $n = 83$ ) varied with mean longitude, as the model  
157 containing this variable was the only model which scored higher than its associated null model (Table 1).  
158 There was a strong tendency for  $\delta^{13}\text{C}$  to decrease as penguins foraged farther east, off the Kerguelen shelf  
159 (Fig. 2). Furthermore,  $\delta^{13}\text{C}$  varied significantly among years as shown by ANOVA analysis (Fig. 3, Table S4).  
160 Similarly, blood  $\delta^{15}\text{N}$  ( $10.1 \pm 0.2 \text{‰}$ ,  $n = 83$ ) varied among years (Fig. 3, Table S4). However, the inter-year  
161 variation in  $\delta^{15}\text{N}$  was less pronounced than with  $\delta^{13}\text{C}$  and only two years (2016 and 2021) were significantly  
162 different from each other according to the Tukey's tests ( $p$  value = 0.02). Overall, there was little variation  
163 in  $\delta^{15}\text{N}$  among individuals ( $\delta^{15}\text{N}$  range: 9.6 – 10.6 ‰). As for the models predicting  $\delta^{15}\text{N}$  using foraging  
164 effort and success variables, none scored higher than their corresponding null model, despite high  
165 variability detected in all these explanatory variables (Table 1).

166

#### 167 *Foraging success*

168 When considering mass gained per day as a response variable, only the model with foraging trip duration  
169 as a fixed effect scored better than its respective null model. Similarly, when PCAs per day was considered  
170 as a response variable, foraging trip duration again was the fixed effect in the only model scoring better  
171 than its respective null model (Table 1).

172

#### 173 **Discussion**

174 The seabird species include both species labelled as diet generalists and specialists. Yet, almost all seabird  
175 species can display a certain level of flexibility, as even specialist species can feed opportunistically on prey  
176 outside of their main diet (e.g. Ancona et al. 2012). This flexibility might be of particular utility when certain  
177 prey types become temporarily scarce. Yet, we found that the King Penguin, a myctophid specialist, does

178 not greatly vary its diet in terms of trophic position ( $\delta^{15}\text{N}$ ), even when encountering highly variable  
179 foraging conditions. Instead, the species relies more on increasing foraging effort to compensate for low  
180 prey capture rates. Our research emphasizes the tight link existing between some marine predators and  
181 their prey, with the conservation of the former being strongly dependant on the latter.

## 182 *Isotopic landscape*

183 A first observation that can be made from our results is that there is a strong longitudinal gradient of  $\delta^{13}\text{C}$   
184 in the environment near Kerguelen. In the Southern Ocean, most reported gradients for this isotope is  
185 usually latitudinal, not longitudinal (Cherel & Hobson 2007, Espinasse et al. 2019). However, the North-  
186 South gradient is evident at a larger scale, while at a smaller scale  $\delta^{13}\text{C}$  is influenced by habitat, with  $^{13}\text{C}$   
187 depleted in offshore habitats relative to coastal habitats (Cherel & Hobson 2007). As the Kerguelen Plateau  
188 extends south of the island to Heard Island (Fig. 2), penguins foraging south will remain in the same shelf  
189 habitat. On the other hand, penguins foraging east will quickly encounter deeper bathymetry, likely  
190 explaining the gradient in  $\delta^{13}\text{C}$  as habitat changes with longitude.

191

## 192 *Diet specialisation*

193 The use of  $\delta^{15}\text{N}$  as a proxy of diet has been controversial when used at a large scale, as spatial gradients of  
194 the isotope exist regardless of trophic position due to variation in baseline  $\delta^{15}\text{N}$  (Seminoff et al. 2012).  
195 However, we did not detect spatial gradients influencing  $\delta^{15}\text{N}$  at a local scale near Kerguelen. It is therefore  
196 a fair assumption that  $\delta^{15}\text{N}$  could be used in this study to assess trophic position of King Penguins, as in  
197 similar studies conducted in the Southern Ocean (Cherel & Hobson 2007, Cherel et al. 2010, Polito et al.  
198 2015). Consequently, we expected  $\delta^{15}\text{N}$  to vary with foraging success in our study. Indeed, low food  
199 availability sometimes causes even specialist species to become more opportunistic in their diet (e.g.  
200 Ancona et al. 2012, Buren et al. 2012). As all alternative prey of King Penguins on Kerguelen islands have

201 a higher  $\delta^{15}\text{N}$  value than their main prey *Krefflichthys anderssoni*, we expected  $\delta^{15}\text{N}$  value of King Penguin  
202 to be higher in low foraging success individuals (Bost et al. 2002, Cherel et al. 2010). Items sometimes  
203 consumed by King Penguins at Kerguelen that have a higher  $\delta^{15}\text{N}$  value include the squid *Gonatus*  
204 *antarcticus* and almost all alternate myctophids prey (see Table S1). Yet, blood  $\delta^{15}\text{N}$  value of foraging  
205 penguins did not increase (or decrease) significantly with the substantially different foraging effort,  
206 foraging success and marine conditions encountered by the penguins. In fact, the  $\delta^{15}\text{N}$  range of  
207 Kerguelen's King Penguins was very narrow across individuals and across years - even when compared to  
208 other seabirds regarded as specialists - suggesting little variation in the diet (see Table 2).

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

218

219 In conclusion, our study shows an example of a strict specialists that seldom adjusts its diet despite the  
220 different conditions encountered, but rather stayed at sea for a longer period to compensate for lower  
221 foraging success. We highly suspect population parameters of such species to be tightly linked to the  
222 availability of its main prey. Indeed, foraging effort cannot increase indefinitely to compensate for low prey  
223 availability, meaning strict specialists might face breeding failures and/or at-sea mortality if prey

224 composition started shifting in the future, especially in the growing context of climatic changes (e.g. Cury  
225 et al. 2011). Ongoing population monitoring efforts are particularly valuable for specialist species, as  
226 population trends might be particularly sensitive to climate change. Long-term prey surveys are also  
227 important to detect such shifts and predict future bottom-up effects affecting seabirds.





228

230 Table 1: Best ranked models explaining  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , mass gained per day and PCAs per day

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

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

234

	 King Penguin (Kerguelen Island) This study	 Chinstrap Penguin (Livingston Island) Polito et al. 2015	 Peruvian Booby (Peru) Renedo et al. 2021	 Guanay Cormorant (Peru) Renedo et al. 2021
<i>Total individuals sampled</i>	n = 83	n = 110	n = 116	n = 122
<i>Number of years sampled</i>	n = 7	n = 5	n = 7	n = 6
<b>Maximum difference between <math>\delta^{15}\text{N}</math> yearly means</b>	<b><math>\Delta 0.45\text{‰}</math></b>	<b><math>\Delta 0.7\text{‰}</math></b>	<b><math>\Delta 2.65\text{‰}</math></b>	<b><math>\Delta 2.55\text{‰}</math></b>
<b>Maximum <math>\delta^{15}\text{N}</math> yearly standard deviation</b>	<b><math>\pm 0.26\text{‰}</math></b>	<b><math>\pm 0.3\text{‰}</math></b>	<b><math>\pm 0.23\text{‰}</math></b>	<b><math>\pm 0.19\text{‰}</math></b>

235

236

237

238 **List of figure captions:**

239

240 Figure 1: Annual variation of foraging effort variables (middle and left graphs) as well as foraging success  
241 variables (right graphs) among equipped King Penguins breeding at Kerguelen Island. Sample sizes  
242 indicate the number of King Penguins sampled. Stars indicate years that were significantly different than  
243 at least two other years when conducting Tukey's tests.

244

245 Figure 2 : Mean diving position of foraging King Penguins during breeding. Each point represents a  
246 penguin's trip. Colors represent blood  $\delta^{13}\text{C}$  of the penguin at the end of the foraging trip, after returning  
247 to the colony. Notice the strong East-West gradients, with blood  $\delta^{13}\text{C}$  values decreasing when penguins  
248 forage off the island's shelf.

249

250 Figure 3 : Annual variation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for blood samples among King Penguins breeding at  
251 Kerguelen Island. Sample sizes indicate the number of King Penguins sampled. Stars indicate years which  
252 were significantly different than at least two other years when conducting Tukey's tests.

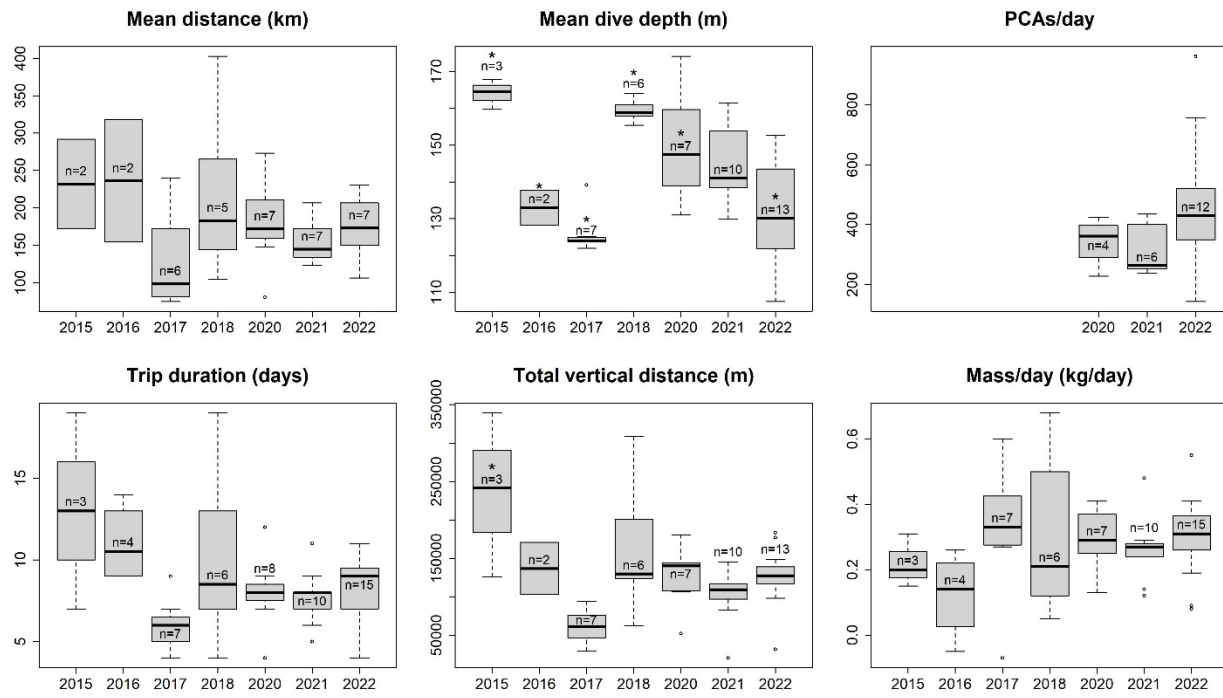


Figure 1

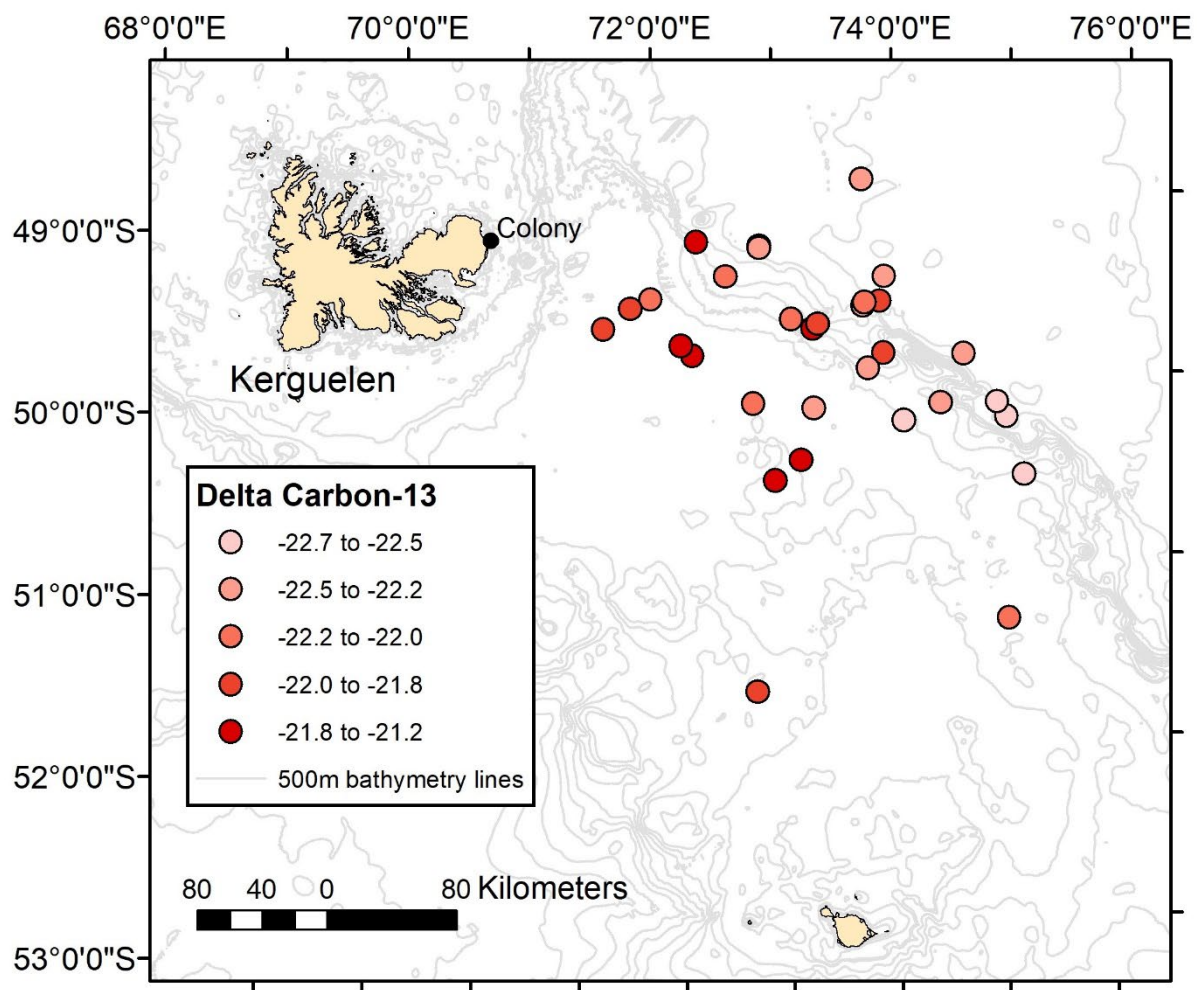


Figure 2

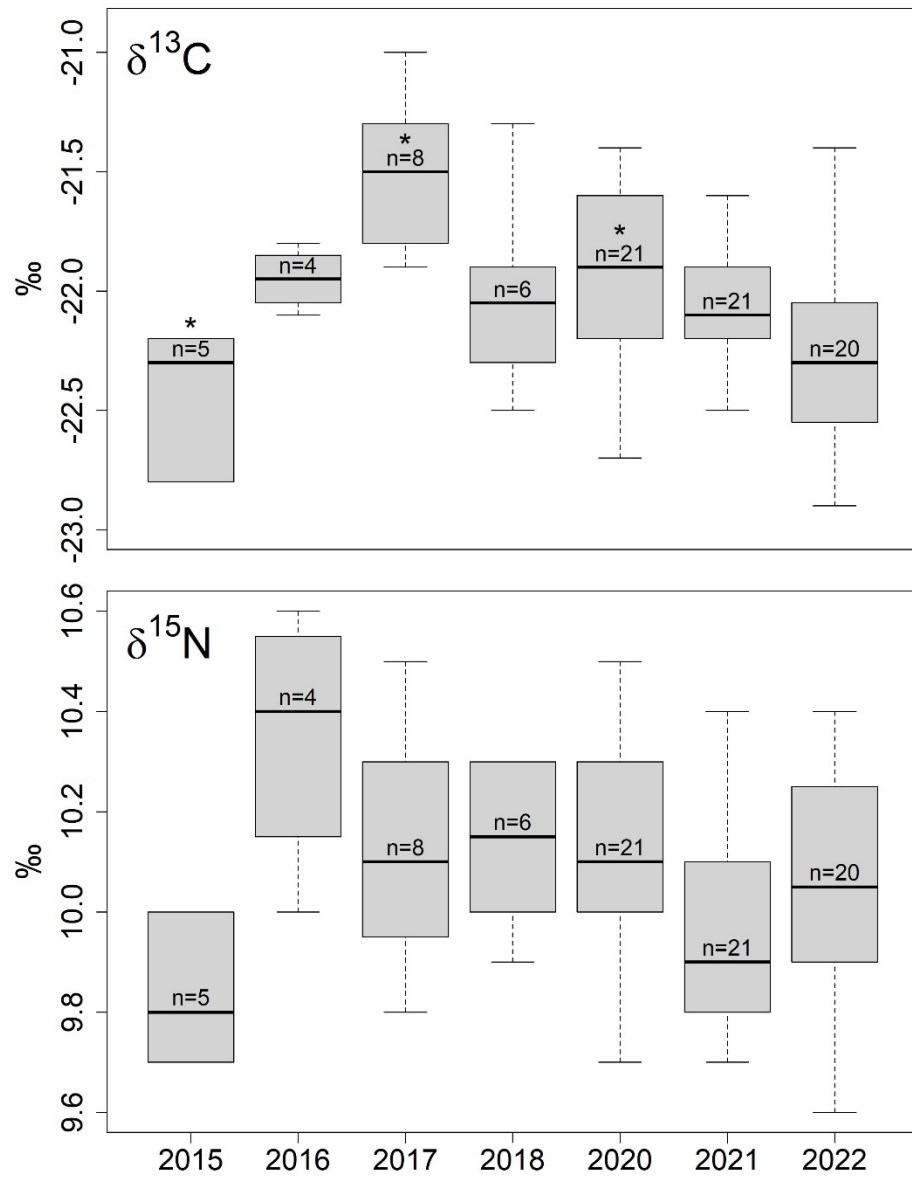


Figure 3

256

257 **Citations**

258

259 Abrams, P. A. (1991). Life history and the relationship between food availability and foraging effort.  
260 Ecology, 72(4), 1242-1252.

261 Adams, N. J., & Klages, N. T. (1987). Seasonal variation in the diet of the king penguin (*Aptenodytes*  
262 *patagonicus*) at sub-Antarctic Marion Island. *Journal of Zoology*, 212(2), 303-324.

263 Ancona, S., Calixto-Albarrán, I., & Drummond, H. (2012). Effect of El Niño on the diet of a specialist seabird,  
264 *Sula neboxii*, in the warm eastern tropical Pacific. *Marine Ecology Progress Series*, 462, 261-271.

265 Barbraud, C., Delord, K., Bost, C. A., Chaigne, A., Marteau, C., & Weimerskirch, H. (2020). Population trends  
266 of penguins in the French Southern Territories. *Polar Biology*, 43, 835-850.

267 Bates D., Mächler M., Bolker B., Walker S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal*  
268 *of Statistical Software*, 67(1), 1–48. doi:10.18637/jss.v067.i01.

269 Bost, C. A., Zorn, T., Le Maho, Y., & Duhamel, G. (2002). Feeding of diving predators and diel vertical  
270 migration of prey: King penguins<sup>1</sup> diet versus trawl sampling at Kerguelen Islands. *Marine Ecology Progress*  
271 *Series*, 227, 51-61.

272 Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, DG, Weimerskirch, H. (2009).  
273 Importance of Southern Ocean fronts for seabird and marine mammals). *Journal of Marine Systems*.  
274 *Special Issue on Processes at Oceanic Fronts of the Journal of Marine Systems (JMS-SIOF)* 79: 363-376.  
275 <https://doi.org/10.1016/j.imarsys.2008.11.022>

276 Bost, C. A., Cotté, C., Terray, P., Barbraud, C., Bon, C., Delord, K., ... & Weimerskirch, H. (2015). Large-scale  
277 climatic anomalies affect marine predator foraging behaviour and demography. *Nature communications*,  
278 6(1), 8220.

279 Breusch, T.S. (1978): Testing for Autocorrelation in Dynamic Linear Models, *Australian Economic Papers*,  
280 17, 334-355.

281 Brisson-Curadeau, É., & Elliott, K. H. (2019). Prey capture and selection throughout the breeding season in  
282 a deep-diving generalist seabird, the thick-billed murre. *Journal of Avian Biology*, 50(7).

283 Brisson-Curadeau, É., Handrich, Y., Elliott, K. H., & Bost, C. A. (2021). Accelerometry predicts prey-capture  
284 rates in the deep-diving king penguin *Aptenodytes patagonicus*. *Marine Biology*, 168, 1-10.

285 Brisson-Curadeau, É., Elliott, K., & Bost, C. A. (2023). Contrasting bottom-up effects of warming ocean on  
286 two king penguin populations. *Global Change Biology*, 29(4), 998-1008.

287 Buren, A. D., Koen-Alonso, M., & Montevecchi, W. A. (2012). Linking predator diet and prey availability:  
288 common murre and capelin in the Northwest Atlantic. *Marine Ecology Progress Series*, 445, 25-35.

289 Charrassin, J. B., & Bost, C. A. (2001). Utilisation of the oceanic habitat by king penguins over the annual  
290 cycle. *Marine Ecology Progress Series*, 221, 285-298.

291 Charrassin, J. B., Park, Y. H., Maho, Y. L., & Bost, C. A. (2002). Penguins as oceanographers unravel hidden  
292 mechanisms of marine productivity. *Ecology Letters*, 5(3), 317-319.

293 Cherel, Y., Pütz, K., & Hobson, K. A. (2002). Summer diet of king penguins (*Aptenodytes patagonicus*) at  
294 the Falkland Islands, southern Atlantic Ocean. *Polar Biology*, 25, 898-906.

295 Cherel, Y., & Hobson, K. A. (2007). Geographical variation in carbon stable isotope signatures of marine  
296 predators: a tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series*,  
297 329, 281-287.

298 Cherel, Y., Hobson, K. A., Guinet, C., & Vanpe, C. (2007). Stable isotopes document seasonal changes in  
299 trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean.  
300 *Journal of Animal Ecology*, 76(4), 826-836.

301 Cherel, Y., Fontaine, C., Richard, P., & Labatc, J. P. (2010). Isotopic niches and trophic levels of myctophid  
302 fishes and their predators in the Southern Ocean. *Limnology and oceanography*, 55(1), 324-332.

303 Cherel, Y., GasCo, N., & Duhamel, G. (2011). Top predators and stable isotopes document the cephalopod  
304 fauna and its trophic relationships in Kerguelen waters. *The Kerguelen Plateau: marine ecosystem and*  
305 *fisheries. Société Française d'Ichtyologie, Paris*, 99-108.

306 Cox, A. R., Robertson, R. J., Lendvai, Á. Z., Everitt, K., & Bonier, F. (2019). Rainy springs linked to poor  
307 nestling growth in a declining avian aerial insectivore (*Tachycineta bicolor*). *Proceedings of the Royal*  
308 *Society B*, 286(1898), 20190018.

309 Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J., Furness, R.W., Mills, J.A., Murphy,  
310 E.J., Österblom, H., Paleczny, M. and Piatt, J.F., 2011. Global seabird response to forage fish depletion—  
311 one-third for the birds. *Science*, 334(6063), 1703-1706.

312 Depot, K.M., Scopel, L.C., Kress, S.W., Shannon, P., Diamond, A.W., & Elliott, K.H. (2020). Atlantic puffin diet  
313 reflects haddock and redfish abundance in the Gulf of Maine. *Marine Ecology Progress Series*, 656, 75-87.

314 Espinasse, B., Pakhomov, E. A., Hunt, B. P. V., & Bury, S. J. (2019). Latitudinal gradient consistency in carbon  
315 and nitrogen stable isotopes of particulate organic matter in the Southern Ocean. *Marine Ecology Progress*  
316 *Series*, 631, 19-30.

317 Fromant, A., Delord, K., Bost, C. A., Eizenberg, Y. H., Botha, J. A., Cherel, Y., ... & Arnould, J. P. (2021). Impact  
318 of extreme environmental conditions: foraging behaviour and trophic ecology responses of a diving  
319 seabird, the common diving petrel. *Progress in Oceanography*, 198, 102676.

320 Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community  
321 interactions under climate change. *Trends in ecology & evolution*, 25(6), 325-331.

322 Hobson, K. A., Piatt, J. F., & Pitocchelli, J. (1994). Using stable isotopes to determine seabird trophic  
323 relationships. *Journal of animal ecology*, 786-798.

324 Jakubas, D., Wojczulanis-Jakubas, K., & Walkusz, W. (2007). Response of dovekie to changes in food  
325 availability. *Waterbirds*, 30(3), 421-428.

326 Jones, T., Parrish, J. K., Peterson, W. T., Bjorkstedt, E. P., Bond, N. A., Ballance, L. T., ... & Harvey, J. (2018).  
327 Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophysical Research*  
328 *Letters*, 45(7), 3193-3202.

329 Le Bohec, C., Durant, J. M., Gauthier-Clerc, M., Stenseth, N. C., Park, Y. H., Pradel, R., ... & Le Maho, Y.  
330 (2008). King penguin population threatened by Southern Ocean warming. *Proceedings of the National*  
331 *Academy of Sciences*, 105(7), 2493-2497.

332 Ludynia, K., Roux, J. P., Jones, R., Kemper, J., & Underhill, L. G. (2010). Surviving off junk: low-energy prey  
333 dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between 1996  
334 and 2009. *African Journal of Marine Science*, 32(3), 563-572.

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

337 Osborne, O.E., Hara, P.D., Whelan, S., Zandbergen, P., Hatch, S.A. & Elliott, K.H. (2020) Breeding seabirds  
338 increase foraging range in response to an extreme marine heatwave. *Marine Ecology Progress Series*, 646,  
339 161-173.

340 Péron, C., Weimerskirch, H., & Bost, C. A. (2012). Projected poleward shift of king penguins'(*Aptenodytes*  
341 *patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proceedings of the Royal Society*  
342 *B: Biological Sciences*, 279(1738), 2515-2523.

343 Pichegru, L., Ryan, P. G., Van Eeden, R., Reid, T., Grémillet, D., & Wanless, R. (2012). Industrial fishing, no-  
344 take zones and endangered penguins. *Biological Conservation*, 156, 117-125.

345 Polito, M. J., Trivelpiece, W. Z., Patterson, W. P., Karnovsky, N. J., Reiss, C. S., & Emslie, S. D. (2015).  
346 Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations  
347 of *Pygoscelis* penguins. *Marine Ecology Progress Series*, 519, 221-237.

348 Quillfeldt, P., McGill, R. A., & Furness, R. W. (2005). Diet and foraging areas of Southern Ocean seabirds  
349 and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Marine*  
350 *Ecology Progress Series*, 295, 295-304.

351 Renedo, M., Point, D., Sonke, J. E., Lorrain, A., Demarcq, H., Graco, M., ... & Bertrand, S. L. (2021). ENSO  
352 climate forcing of the marine mercury cycle in the Peruvian upwelling zone does not affect methylmercury  
353 levels of marine avian top predators. *Environmental Science & Technology*, 55(23), 15754-15765.

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

357 Scopel, L., Diamond, A., Kress, S., & Shannon, P. (2019). Varied breeding responses of seabirds to a regime  
358 shift in prey base in the Gulf of Maine. *Marine Ecology Progress Series*, 626, 177-196.

359 Seminoff, J. A., Benson, S. R., Arthur, K. E., Eguchi, T., Dutton, P. H., Tapilatu, R. F., & Popp, B. N. (2012).  
360 Stable isotope tracking of endangered sea turtles: validation with satellite telemetry and  $\delta^{15}\text{N}$  analysis of  
361 amino acids. *PLoS one*, 7(5), e37403.

362 Sydeman, W.J., Schoeman, D.S., Thompson, S.A., Hoover, B.A., García-Reyes, M., Daunt, F., Agnew, P.,  
363 Anker-Nilssen, T., Barbraud, C., Barrett, R. and Becker, P.H., 2021. Hemispheric asymmetry in ocean change  
364 and the productivity of ecosystem sentinels. *Science*, 372(6545), 980-983.

365 Venables, W. N. and Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer-Verlag.

366 Zeileis A., Hothorn T. (2002). Diagnostic Checking in Regression Relationships. R News, 2(3), 7–10.

367 <https://CRAN.R-project.org/doc/Rnews/>.

368

369

370 Table S1:  $\delta^{15}\text{N}$  values of alternate prey items of king penguins at Kerguelen, in comparison with the main  
 371 prey, *Krefflichthys anderssoni*

372

Prey item	$\delta^{15}\text{N}$ (‰)	Source
<b><i>Krefflichthys anderssoni</i></b>	<b>7.6 ± 0.2</b>	<b>Cherel et al. 2010</b>
<i>Protomyctophum bolini</i>	9.2 ± 0.4	Cherel et al. 2010
<i>Electrona carlsbergi</i>	9.5 ± 0.2	Cherel et al. 2010
<i>Protomyctophum tenisoni</i>	8.1 ± 0.3	Cherel et al. 2010
<i>Protomyctophum andriashevi</i>	8.7 ± 0.4	Cherel et al. 2010
<i>Electrona antarctica</i>	8.9 ± 0.3	Cherel et al. 2010
<i>Martialia hyadesi</i>	7.7 ± 0.6	Cherel et al. 2011, Hobson & Cherel (2006)
<i>Gonatus antarcticus</i>	13.3 ± 0.5	Cherel et al. 2011, Hobson & Cherel (2006)

373

374

375 Table S2: Loggers used from 2015-2022

Model name	Company	Company location	Information recorded by logger			
			GPS	Depth	3D acceleration	Temperature
FastLoc	SirTrack Ltd	Havelock North, NZ	x			
PTT Kiwisat	SirTrack Ltd	Havelock North, NZ	x			
MK9	Wildlife Computer	Redmond, US		x		x
Axy-Trek	Technosmart	Colleverde, It	x	x	x	x
Axy 4 XS	Technosmart	Colleverde, It			x	

376

377

378

379 Table S3: deployment by year

Year	Deployment
2015	3 birds equipped with both FastLoc and Mk9
2016	2 birds equipped with both FastLoc and Mk9 2 bird equipped with FastLoc only
2017	7 birds equipped with both FastLoc and Mk9
2018	6 birds equipped with both FastLoc and Mk9
2020	3 birds equipped with both PTT Kiwisat and Mk9 4 birds equipped with Axy-Trek
2021	7 birds equipped with Axy-trek 3 birds equipped with MK9
2022	8 birds equipped with Axy-trek 7 birds equipped with both Axy 4XS and MK9

380

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

Model	Mean of residuals	Pearson correlation test between residuals and independent variable	Autocorrelation coefficient of the residuals	Breush Pagan Test (Homoskedasticity of residuals)
$\delta^{13}\text{C} \sim$ Mean longitude of foraging dives ( $^{\circ}$ )	<0.0001	t = 3.873e-11 df = 32 p-value = 1	0.14	BP = 2.3353 df = 1 p-value = 0.1265
Mass $\sim$ Foraging trip duration (days)	<0.0001	t = -1.167e-14 df = 48 p-value = 1	-0.13	BP = 1.1619 df = 1 p-value = 0.2811
PCA $\sim$ Foraging trip duration (days)	<0.0001	t = 4.652 e-15 df = 26 p-value = 1	-0.31	BP = 0.55567 df = 1 p-value = 0.456

382

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

Variable	Degrees of freedom	F value	p-value
$\delta^{13}\text{C}$	6	7.375	<0.001
$\delta^{15}\text{N}$	6	2.971	0.01
Mean distance to colony	6	1.406	0.25
Trip duration	6	3.294	0.009
Mean depth	6	9.769	<0.001
Total vertical distance	6	5.196	<0.001
PCAs per day	2	2.088	0.15
Mass gained per day	6	1.049	0.41

385

386