



HAL
open science

COVID-related anthropause highlights the impact of marine traffic but not tourists on breeding little penguins

Benjamin Dupuis, Akiko Kato, Nicolas Joly, Claire Saraux, Yan Ropert-coudert, Andre Chiaradia, Marianna Chimienti

► To cite this version:

Benjamin Dupuis, Akiko Kato, Nicolas Joly, Claire Saraux, Yan Ropert-coudert, et al.. COVID-related anthropause highlights the impact of marine traffic but not tourists on breeding little penguins. *Biological Conservation*, 2023, 287, pp.110323. 10.1016/j.biocon.2023.110323 . hal-04256189

HAL Id: hal-04256189

<https://hal.science/hal-04256189v1>

Submitted on 15 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.



Distributed under a Creative Commons Attribution 4.0 International License

1 **COVID-related anthropause highlights the impact of marine traffic on breeding little**
2 **penguins**

3

4 Benjamin Dupuis¹, Akiko Kato¹, Nicolas Joly², Claire Saraux², Yan Ropert-Coudert¹, Andre
5 Chiaradia^{3,4}, Marianna Chimienti¹

6 Affiliations:

7 1 - Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS—La Rochelle Université, 79360

8 Villiers en Bois, France

9 2 - Université de Strasbourg, CNRS, Institut Pluridisciplinaire Hubert Curien (IPHC), UMR 7178,

10 23 rue Becquerel, 67000 Strasbourg, France

11 3 - Conservation Department Phillip Island Nature Parks, Cowes, VIC 3922, Australia

12 4 – School of Biological Science, Monash University, Clayton, Australia

13 **Impact statement:**

14 We found that marine traffic, but not tourist presence, negatively impact the foraging and
15 provisioning behavior of little penguins.

16

17 **Abstract:**

18 The COVID-19 pandemic and its lock-down measures have resulted in periods of reduced human
19 activity, known as anthropause. While this period was expected to be favorable for the marine
20 ecosystem, due to a probable reduction of pollution, shipping traffic, industrial activity and fishing
21 pressure, negative counterparts such as the increased use of disposable plastic and reduced fisheries
22 surveillance and enforcement could counterbalance these positive effects. Simultaneously, on-land
23 pressure due to human disturbance and tourism should have drastically decreased, potentially
24 benefiting land-based marine breeders such as seabirds. Thus, long-term datasets became crucial to
25 differentiate between historical trends and any evident changes resulting from the anthropause. We
26 analyzed 11 years of data on several biological parameters of little penguins (*Eudyptula minor*)
27 from the Penguin Parade ®, a popular tourist attraction at Phillip Island, Australia. We investigated
28 the impact of anthropogenic activities on penguin behavior during the breeding season measured by
29 (1) distribution at sea, (2) colony attendance, (3) isotopic niche (4) chick meal mass, and (5)
30 offspring investment against shipping traffic and number of tourists. The 2020 lock-downs resulted
31 in a near absence of tourists visiting the Penguin Parade ®, which was otherwise visited by
32 800,000+ visitors on average per year. However, our long-term analysis showed no effect of the
33 presence of visitors on little penguins' activities. Surprisingly, the anthropause did not triggered any
34 changes in maritime traffic intensity and distribution in the region. While we found significant
35 inter- and intra-annual variations for most parameters, we detected a negative effect of marine
36 traffic on the foraging efficiency. Our results suggest that environmental variations have a greater
37 influence on the breeding behavior of little penguins compared to short-term anthropause events.

38 Our long-term dataset was key to test whether changes in anthropogenic activities affected the
39 wildlife during the COVID-19 pandemic.

40

41 **Keywords:** COVID-19 lock-down, Long-term monitoring, Anthropogenic activities, Breeding
42 ecology, Little penguins

43 **Introduction**

44 With the development of human activities, ecosystems can no longer be considered as undisturbed
45 and independent entities (Mace, 2014), leading to the concept of socio-ecological systems (Everard,
46 2020; Wei et al., 2018). Because of the numerous interactions at stake, socio-ecological ecosystems
47 are often complex to analyze (Sugihara et al., 2012). The quasi-continuous presence of humans in
48 most, if not all, ecosystems makes it challenging to understand the full impact of anthropogenic
49 activities on the environment.

50 In 2020, the COVID-19 pandemic led to periods of lock-downs that resulted in a major
51 reduction of human activities and movement at both local and global level, a period coined as the
52 “anthropause” (Lamers & Student, 2021; Rutz et al., 2020). The anthropause created an opportunity
53 to quantify the impact of human activities on wildlife. To date, studies found both negative and
54 positive effects of this anthropause on wildlife, through for example, increase of predators presence
55 and disturbance on an iconic seabird colony in the Baltic Sea (Hentati-Sundberg et al., 2021), as
56 well as increased species richness in less-disturbed areas (Manenti et al., 2020). Lock-downs also
57 led to increased illegal hunting and plastic pollution, and reduced conservation efforts with negative
58 effects on wildlife (Bates et al., 2021; Kadykalo et al., 2022). In a comparative study, Bates et al.
59 (Bates et al., 2021) showed that despite the decrease in humans’ movement, or industrial activities,
60 the median responses of wildlife to anthropause were centered on 0, because firstly positive and
61 negative effects balanced themselves, while for numerous species, no changes were observed.

62 Moreover, it can be misleading to consider that the anthropause is a phenomenon homogeneously
63 distributed across the globe. The decrease in human activities was not equal across the planet (Bates
64 et al., 2021). Keeping in mind the level of variation of anthropauses, and eventual anthropulses (i.e.
65 increase of human activities) it is key to study effects of these periods on ecosystems.

66 It can be complex to study the dynamics of entire ecosystems, specifically within the context of the
67 COVID lock-down, considering the difficulties to carry on with species and habitat monitoring
68 activities during these periods. Monitoring “sentinel species” helps tackling this issue. Sentinel

69 species integrate changes happening across ecosystems' levels (Durant JM et al., 2009), integrate
70 broader processes into rapidly interpretable metrics, are simpler to study, can respond rapidly to
71 environmental changes and cover a large spatial scale (Bost et al., 2008; Durant JM et al., 2009;
72 Hazen et al., 2019; Siddig et al., 2016). Therefore, long-term dataset on marine predators, especially
73 seabirds, are often used as indicators of ecosystems' changes (Cairns, 1988; Furness &
74 Camphuysen, 1997; Piatt, Sydeman, et al., 2007).

75 Data collection via continuous monitoring programs allows researchers to compare the pace of
76 parameters responses to global changes and assess effects of human pressure on wild populations
77 (Cairns, 1988; Durant JM et al., 2009; Einoder, 2009; Ramírez et al., 2017; Tucker et al., 2018,
78 2019). Techniques used vary depending on the research question and feasibility, comprising of
79 visual observations, counts, nest monitoring, blood sampling and use of bio-logging techniques. In
80 seabirds, chick growth, colony attendance, and individuals' activity budgets vary at different
81 temporal scales and in relation to both environmental and human activities (Cairns, 1988).
82 Depending on the specific effects of the COVID lock-downs and the relative short period these
83 were put in place, some of these traits might show no responses to anthropogenic activities (Cairns,
84 1988; Piatt, Harding, et al., 2007).

85 During breeding season, seabirds are central place foragers exploiting food resources around
86 their breeding colony to which they return due to reproductive requirements (e.g. egg incubation,
87 chick provisioning), hence alternating between nest attendance and foraging trips (Einoder, 2009;
88 Piatt, Sydeman, et al., 2007; Saraux et al., 2011). Seabirds must cope with constraints of living in
89 two different environments, feeding at sea and breeding on land, making them exposed and
90 vulnerable to threats from both land and sea. The little penguin (*Eudyptula minor*) is the smallest
91 penguin species endemic of Australia and New Zealand (BirdLife International, 2023). Phillip
92 Island, Australia, holds one of the largest little penguin colonies in the world with a population
93 estimated between 28,000 and 32,000 individuals (Sutherland & Dann, 2014). The colony located at
94 the "Penguin Parade ®" receives the visit of hundreds of thousands of tourists per year, especially

95 when little penguins return ashore at night (Dann & Chambers, 2013). At sea, little penguins can
96 also interact with maritime traffic such as commercial shipping, recreational or commercial fishing
97 vessels (Cannell et al., 2020; Crawford et al., 2017). Land introduced predators and starvation are
98 the major causes of little penguins' mortality, but collision with vessels were also reported (Cannell
99 et al., 2016, 2020), even though their foraging range is small (around 30 km for single day trips but
100 can be up to 214 km for multi days trips) (Collins et al., 1999; Poupart et al., 2017; Sánchez et al.,
101 2018).

102 On land, tourism has been shown to affect various parameters of penguins' ecology such as stress
103 level, reproductive output (Ellenberg et al., 2007) or behavior (Colombelli-Négrel & Katsis, 2021;
104 Ellenberg et al., 2007; French et al., 2019). At-sea, vessels can directly (Pichegru et al., 2022) or
105 indirectly (Mattern et al., 2013) affect penguins foraging through noise pollution and deterioration
106 of the environment, respectively. During the COVID-19 pandemic, Australia underwent a series of
107 rigid lock-downs, drastically reducing anthropogenic activities. During most of that period, the
108 "Penguin Parade ®" remained closed to the tourists, providing a good opportunity to understand if
109 the anthropause affected ecology of little penguins.

110 We investigated whether the anthropause affected metrics linked to little penguin's behavior during
111 the breeding season in 2020 (year with lock-downs) by comparing against 10 years of population
112 monitoring and movement data (2010-2019) to 2020. The studied colony has been monitored for
113 the past 23 years using an automated penguin monitoring system (date, time and weight of penguins
114 recorded when leaving and arriving to the colony), with daily count of penguins arrival at dusk, and
115 with the use of bio-logging techniques (the latter since 2010) (Chiaradia & Kerry, 1999; Ramírez et
116 al., 2015). We tested whether reduced anthropogenic activities influenced little penguins (1) at-sea
117 activity by studying their at-sea distribution, overlap with marine traffic, isotopic diet (in terms of
118 prey type and quantity), and (2) on-land activity by studying their colony attendance (departure and
119 arrival time), and meal size given to their chicks. We considered the daily number of tourists at the
120 Penguin Parade ® as a proxy of land disturbance, and the number of vessels and their overlap with

121 little penguins' foraging area at-sea as a proxy of the at-sea disturbance. We hypothesized that when
122 land disturbance is reduced during the anthropause, due to the absence of tourists in the parks, little
123 penguins would change their colony attendance pattern by coming and leaving more synchronously,
124 as they will not have to avoid tourist disturbance (Klomp & Wooller, 1991; Rodríguez et al., 2016).
125 Moreover, if the anthropause reduced the at-sea disturbance, little penguins would display a higher
126 foraging efficiency as the overall marine environment and its species will less be disturbed by the
127 traffic, through reduction in noise pollution for instance (Pichegru et al., 2010, 2017).

128 **Material and Methods**

129 Study site and long-term monitoring of foraging behavior

130 The study was conducted on the little penguin breeding colony at Phillip Island, Australia (38°21'S,
131 145°09'E) from 2010 to 2020. The breeding season of little penguins occurs in the austral spring
132 and summer, from September to December.

133 For the period of our study (11 breeding seasons, 2010-2020), penguins were captured from their
134 nest boxes and equipped with GPS loggers (Axy-Trek, Italy, Mr Lee, China) recording positions at
135 120 s interval for incubation and postguard trips and every 20 s for guard trips (table 1). Loggers
136 were attached to their lower backs with Tesa® tape (Wilson et al., 1997). After returning from their
137 foraging trips, penguins were recaptured at the colony and the logger retrieved. Handling time was
138 kept at less than 5 min. Details of the logger deployment are described in Pelletier et al. (2014),
139 Sanchez et al. (2018) and Barreau et al. (2021) (Barreau et al., 2021; Pelletier et al., 2014; Sánchez
140 et al., 2018). We combined the information obtained from GPS data for estimating the distribution
141 of little penguins at sea, stable isotopes data to investigate their diet, as well as from the automated
142 monitoring system to track changes in body weight and colony attendance.

143 Two automated penguin monitoring systems (APMS) are placed on the main pathways between the
144 little penguins' colony and the beach. When walking through APMS, little penguins are
145 individually identified with passive transponders (Allflex, Australia) that had previously been
146 inserted in the back of the penguins, either as chicks or the first time they were encountered in the
147 colony. In addition, APMS record date, time, direction of passage, and the body mass of the
148 individuals (Joly et al., 2022).

149 This research was conducted under the Phillip Island Nature Parks Animal Experimentation Ethics
150 Committee approval and a research permit issued by the Department of Environment Land, Water
151 and Planning of the state of Victoria, Australia.

152 Data manipulation and analysis

153 Data manipulation and analysis was done in R v4.2.3 (R Core Team, 2023). All scripts used in this
154 analysis are available upon request (Github link removed for anonymity). Unless specified
155 otherwise, results indicate mean and standard error. As well, when more than one variable was
156 considered within a model, all model combinations were tested, and we performed model selection
157 using Akaike's information criterion (AIC) (Bozdogan, 1987). The model with the lowest AIC was
158 considered as best. Normality of residuals, residual autocorrelation and homoscedasticity were
159 checked graphically. We considered p-values under 0.05 as significant. Unless stated otherwise,
160 pairwise post-hoc comparisons were performed using Holm p-value correction (Holm, 1978).

161

162 GPS data processing

163 A foraging trip was defined as a period from the departure to the return to the colony. Because little
164 penguins are visual hunters, foraging activities only occur during daylight (Cannell & Cullen, 1998;
165 Chiaradia et al., 2007). Their foraging trips last typically between 1-9 days during incubation (Kato
166 et al., 2008), 1 day during guard (Pelletier et al., 2014) and between 1-17 days during post-guard
167 (Saraux et al., 2011). From each foraging trip, and day out at sea, we extracted a "foraging
168 segment", intended as the period between nautical dawn and nautical dusk. Therefore, one-day trip
169 contained only one foraging segment, while multiple-days trip could contain several segments. We
170 removed foraging segments with less than 3 GPS locations, and segments starting after sunrise or
171 stopping before sunset, from the analysis. Overall, out of 233 foraging trips, a total of 371 foraging
172 segments were extracted and analyzed (range 1-7 segments per individual).

173 We calculated the distance between each consecutive location on the WGS ellipsoid using the
174 *pointdistance()* function from the "raster" R package (Hijmans, 2022). Swimming speed was then
175 calculated between two consecutive locations as the distance divided by the time interval.
176 Furthermore, we excluded GPS locations with swimming speed higher than 8 km.h⁻¹ (i.e. max
177 swimming speed of little penguins, (Watanuki et al., 2006)), or with a time interval between 2
178 consecutive GPS locations lower than 7.2 sec (i.e. duplicated points). GPS locations can be obtained

179 only when penguins resurface, therefore it is necessary to interpolate raw GPS data and reconstruct
180 their path. For each foraging segment, we regularized the time interval between each location by
181 performing spatial interpolation at 15-min interval using the correlated random walk algorithm
182 within the *crawlWrap()* function from “MomentuHMM” R package (McClintock & Michelot,
183 2018).

184 Interpolated foraging segments were projected into the GDA94 / Australian Albers projection. For
185 each breeding season, we then used the *kernelUD()* function from the “adehabitatHR” R package
186 (Calenge, 2006) to calculate 50% (core area), and 95% (homerange) kernel utilization distribution
187 (UD). The smoothing parameter *h* was calculated using the ad hoc method (Seaman et al., 1998).

188

189 Stable isotope data processing

190 To describe the isotopic niches of little penguins and examine differences between 2020 and
191 previous years (2010-2019), we analyzed $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotopes from 842 blood samples
192 ($n = 196$ in incubation, $n = 367$ in guard, $n = 279$ in post-guard). Values in $\delta^{15}\text{N}$ increase with prey
193 trophic level, while $\delta^{13}\text{C}$ values are higher inshore than offshore (Hobson et al., 1994). We
194 followed the protocol described in Chiaradia et al. (Chiaradia et al., 2016). Whole blood was freeze-
195 dried and then powdered. As mass C/N ratios were all below 3.5, there was no need for correction
196 of lipid contents in whole blood (Post et al., 2007). Isotopic analysis was then performed by means
197 of a Robo-Prep elemental analyzer coupled to a Europe 20:20 continuous-flow isotope ratio mass
198 spectrometer. Based on replicate measurements of within-run standards, measurement error was
199 estimated to be ± 0.3 and $\pm 0.1\%$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements, respectively.

200

201 Automated penguin monitoring system

202 We evaluated two measures of body mass variation. First, we calculated the mass gained after a
203 foraging trip, which we considered to be an estimate of foraging efficiency (Saraux et al., 2011).

204 Two body masses were considered belonging to the same foraging trip when their records were

205 consecutive in date and time for a given transponder number and the trip duration was not longer
206 than 1 d in guard and 17 d in incubation and post-guard (Salton et al., 2015). Then, for post-guard
207 only, we calculated the overnight mass variation after returning from a foraging trip, which we
208 considered to be an estimate of chick provisioning during chick-rearing. During this stage, little
209 penguins stay only a few hours in the colony, so we assumed that all body mass loss was due to
210 chick provisioning. Body mass gained at sea was only considered when ranging from 700 to 1700 g
211 and body mass change from -75 to 500 during incubation and 0 to 600 g during guard and post-
212 guard (Joly et al., 2022; Saraux et al., 2011).

213 Using APMS, we also calculated penguins' attendance to the colony. When penguins crossed the
214 weighbridge, it registers the timestamp, and transponder number of the penguin, allowing us to now
215 departure and arrival times of each foraging trips. We calculated departure and arrival times relative
216 to nautical dawn and dusk, respectively, to account for variation in day length (Rodríguez et al.,
217 2016).

218

219 Proxies of anthropogenic activities

220 Given that little penguins breed on land and forage at sea, we defined both on land and at sea
221 indicators of anthropogenic activities. The number of tourists present each night was used as an
222 index of human activity on land. This number was monitored daily between 2010 and 2020. Over
223 the studied period, artificial lighting (orange halogen lights, 3 lux) was used to enhance visibility of
224 penguins for tourists. These lights were turned on from sunset to 1.5 h after the arrival of the first
225 penguins (Rodríguez et al., 2016). During the COVID lock-downs, these lights were still in place
226 but without the presence of tourists.

227 For the activity at sea, we used the number of vessels (fishing, commercial and leisure)
228 within the little penguin foraging area (longitude 145 to 146°E, latitude 38.5 to 39.5°S) during their
229 breeding season (September to December). We used the open-source dataset from the Australian
230 Marine Safety Authority (<https://www.operations.amsa.gov.au/Spatial/DataServices/DigitalData>)

231 and for each vessel we obtained its ID, latitude, longitude, type and timestamp. As vessels transmit
232 their locations at different time interval (from one per 15 minutes to once a day), we built daily
233 indices by keeping only one location per vessel and day: the closest to noon available. Data were
234 available only between 2014 and 2020. Information earlier than 2014 was not considered because of
235 the lower time resolution compared to later data, and data for November 2019 was missing.
236 Hereafter, we refer to the number of vessels within little penguin foraging grounds as the marine
237 traffic intensity. We calculated marine traffic UD using the same method described before for the
238 little penguins.

239

240 Statistical analysis

241 *Variation of anthropogenic activities :*

242 Using linear models, we investigated the variation of the number of vessels in little penguins
243 foraging area and the number of tourists at the penguin parade ® between months and years. Then,
244 using pairwise post-hoc comparison, we tested the difference between the COVID year (2020) and
245 the previous years.

246

247 *Spatial variation of at sea distribution and overlap with marine traffic*

248 Overlap analyses were performed using the Utilization Distribution Overlap Index (UDOI, (Fieberg
249 & Kochanny, 2005)) which quantifies the pattern of space-use as a function of the product of the
250 overlapping UDs. UDOI is equal to 0 when two UDs do not overlap and to 1 if the UDs are
251 completely overlapping and uniformly distributed. Values higher than 1 indicate higher normal
252 overlap relative to uniform space-use. UDOI were calculated using the *kerneloverlap()* function
253 from the “adehabitatHR” R package (Calenge, 2006).

254 We calculated the UDOIs of the 95% UD of the at sea distributions of penguins for all years. We
255 calculated the UDOIs of a year A with all the other years, generating a distribution of UDOIs for
256 year A. We then assessed whether the observed distribution in 2020 was different compared to the

257 previous years. We also calculated the UDOI between little penguins and marine traffic. Again, we
258 calculated UDOIs of year A (little penguin) with all the available years (marine traffic). We
259 obtained distributions of the UDOIs between little penguins and marine traffic. We tested
260 differences between years using generalized linear models (GLMs) with a gamma distribution. We
261 then performed post-hoc pairwise comparison to assess the significance of differences observed
262 between 2020 and the other years.

263

264 *Effect of number of tourists on little penguins attendance and foraging efficiency*

265 Linear models (LMs) were used to test the effect of lock-down on (a) average departure and arrival
266 times of little penguin relative to nautical dawn and nautical dusk, respectively and (b) average
267 mass variation per day over a foraging trip, and overnight. Models were built using the ‘nlme’ R
268 package (Pinheiro et al., 2021). For both models (a and b) we considered number of tourists and
269 number of vessels as explanatory variables, and breeding stage and season as fixed effects. To
270 assess the effect sizes of both vessels and tourists counts, we standardized these data (see equation
271 1).

$$Std_x = \frac{x - mean(x)}{sd(x)} \quad (1)$$

272

273 *Quantification of isotopic niche:*

274 We computed standard ellipse area corrected for small sample size and extreme values (SEA_C) to
275 estimate isotopic niche width and overlap among the different years and breeding stages. SEA_C
276 represents the isotopic niche width of 40% of typical individuals within the groups, based on
277 bivariate normal distribution. The overlap in SEA_C was calculated for all pairs of years within a
278 breeding stage following (Catry et al., 2016) where isotopic niche overlap was expressed as a
279 proportion of the area of overlap between two SEA_C to its own SEA_C . We also computed Bayesian
280 Standard ellipse area (SEA_B) (n = 20000 iterations) to obtain credible intervals (99%, 95% and
281 50%) for the calculated ellipses. We considered non-overlapping 95% CI around SEA_B as an

282 indicator of statistically significant difference between niches width. For all this analysis, we
283 followed the method described in (Jackson et al., 2011) and the 'SIBER' R package.

284 **Results**

285 Variation of anthropogenic activities

286 In 2020, during the COVID lock-downs, Phillip island nature park remained closed for most of the
287 breeding season, resulting in number of tourists 10 times lower than usual (180.4 ± 27.9 tourists per
288 day in 2020 vs. 1770.0 ± 20.5 on average in 2010-2019, all $p < 0.001$, figure 1, supplementary table
289 1.A and 2.A).

290 In 2020, the daily average number of vessels recorded at sea was 262 ± 8.51 . This was significantly
291 higher than the one recorded for 2014 of 212 ± 5.35 (estimate = 50.607, $t = 5.562$, $p < 0.001$), and
292 lower than 2018 with 297 ± 6.91 vessels (estimate = -34.279, $t = -3.767$, $p = 0.002$, figure 1,
293 supplementary table 1.B and 2.B).

294

295 Spatial variation of at sea distribution and overlap with marine traffic

296 While spatial distribution of marine traffic remained similar across seasons, little penguins core
297 (50% UD) and home ranges (95% UD) showed great inter-annual variation across the studied
298 period (figure 2). We compared the overlaps of penguins distribution in 2020 (average UDOI of
299 0.86 ± 0.07) to all the other years (average UDOI ranging from 0.58 ± 0.09 in 2015 in to $1.09 \pm$
300 0.07 in 2014) at 95% UD. We did not find any significant difference in the overlap distributions in
301 2020 vs any other season (supplementary table 1.C and 2.C).

302 Model selection pointed at the model with the effect of the *year* as explanatory variable as best
303 (supplementary table 1.D). We found variation in the overlap between marine traffic and little
304 penguins' distributions (from 2014 to 2020). In 2020, the overlap between little penguins and
305 marine traffic was significantly lower (0.184 ± 0.009) than in 2018 (average = 0.649 ± 0.144 ,
306 estimate = 3.879, $p < 0.001$) and 2017 (average = 0.358 ± 0.128 , estimate = 2.627, $p < 0.001$), but
307 higher than the one of 2015 (average = 0.021 ± 0.003 , estimate = - 41.868, $p < 0.001$, supplementary
308 table 2.D).

309

310 Effect of number of tourists and marine traffic on colony attendance

311 Little penguins left the colony on average 52.9 ± 0.5 minutes ($n = 11116$) before nautical dawn and
312 there is no difference across seasons. The best model testing the effect of anthropogenic activities
313 on the time of departure relative to nautical dawn retained only the effect of breeding stage as
314 explanatory variable (supplementary table 1.E, p -value < 0.01), with therefore no significant inter-
315 annual variations (supplementary table 2.E). During incubation, penguins left 31.8 minutes (95% CI
316 [24.5; 39.0]) before nautical dawn, compared to 74.9 minutes (95% CI [67.7;82.2]) during guard
317 and 47.1 minutes (95% CI [39.9;54.4]) during post-guard (figure 3A).

318 Model selection for the models testing the effect of anthropogenic activities on the time of arrival
319 relative to nautical dusk pointed at the null model as best (supplementary table 1.F), indicating an
320 absence of effect of tourists presence and marine traffic on colony attendance. Penguins showed
321 highly synchronized arrival time regardless of season or breeding stage, arriving at the colony on
322 average 8.2 ± 0.4 min after nautical dusk ($n = 11087$, figure 3B, supplementary table 2.F).

323

324 Effect of number of tourists and marine traffic on foraging efficiency

325 Over a foraging trip, penguins gained on average 258.65 ± 1.75 g per day ($n = 6617$). The best
326 model testing the effect of anthropogenic activities and temporal variations on mass gained per day
327 at sea retained breeding stage and daily average number of vessels at sea as explanatory variables
328 (figure 3, supplementary table 1.G), indicating an effect of marine traffic intensity but not of
329 anthropause on foraging efficiency. Higher number of vessels was associated with lower mass gain
330 at sea for little penguins (estimate = $- 56.9 \pm 17.3$ g, $F = 10.8$, $p = 0.004$, supplementary table 2.G).
331 Predicted breeding stage mass gain were all significantly different from one another ($F = 46.6$, all p
332 < 0.05). During incubation, penguins gained 127.4 g (95% CI [100.6;154.3]) per day, compared to
333 300.7 g (95% CI [274.2;327.1]) in guard, and 261.4 g (95% CI [234.6;288.2]) in post-guard.

334 The average overnight mass change during post-guard, i.e. meal size, was of 278.6 ± 0.1 g ($n =$
335 1794). Though the best model was the one with the average number of vessels at sea

336 (supplementary table 1.H), its effect was not significant on meal size given to the chicks (estimate =
337 - 22.8 ± 11.2, $F = 4.2$, $p = 0.06$, figure 3D, supplementary table 2.H).

338

339 Quantification of isotopic niche

340 A total of 842 blood samples were collected from little penguins across the different breeding stages
341 (supplementary table 3). We observed variations in the isotopic niche values and areas at different
342 breeding stages over 10 years (figure 4). During incubation, the SEAb mode of 2020 was 0.79 ‰²
343 with 95% CI [0.48;1.25] and was significantly higher than 2 other years, 2011 (0.19 ‰² [0.13;0.31])
344 and 2015 (0.21 ‰² [0.14;0.34] (figure 5). During the guard stage, SEAb was higher for 2020
345 (0.98 ‰² [0.69; 1.39] than 2011 again (0.24 ‰² [0.17;0.33]), and 2010 (0.46 ‰² [0.33;0.65].
346 Finally, during the post-guard, the SEAb of 2020 decreased (0.60 ‰² [0.45;0.87]). It was still
347 significantly higher than the SEAb of 2011 (0.29 ‰² [0.21;0.42]), but also significantly lower than
348 the one of 2014 (1.51 ‰² [0.88; 2.72]). These inter annual variations lead to low overlap between
349 the isotopic niches of little penguins between 2010 and 2020 (table 2).

350 **Discussion**

351 Humans have increasingly altered natural habitats, triggering changes in movements, habitat
352 use and population dynamics in wild species (Duhem et al., 2008; Holles et al., 2013; Margalida et
353 al., 2014). The anthropause period caused by the COVID-19 pandemic set an unprecedented
354 opportunity to study the effects of reduced human activities on the biology and ecology of a range
355 of species (Rutz et al., 2020). During the anthropause, human activity on land decreased massively
356 in our studied area, with a reduction almost by a factor 10 in the number of tourists of the Penguin
357 Parade®, Phillip Island Nature Park, Australia. Contrary to the expected (Bates et al., 2021), the
358 lock-down policy did not seem to affect the marine traffic, neither spatially nor quantitatively
359 within the penguin foraging zone within our study site in Bass Strait. This specific setup allowed us
360 to specifically study the effect of on land activity through a stable at-sea potential pressure
361 throughout the study period. Despite the important inter-annual variability in at-sea distribution and
362 diet of little penguins over the studied period (2010-2020), no effect of the anthropause was found.
363 Still, we found anthropogenic effect not linked with the anthropause. Despite the marine traffic
364 intensity stability over the studied period, thanks to our long-term data set, we were able to identify
365 a negative relationship between marine traffic intensity and mass gained at sea per day by little
366 penguins.

367 Human activities are known to affect seabirds' physiology and behaviour. Previous studies
368 showed the negative effects of anthropogenic noise (Pichegru et al., 2017), human presence
369 (Ellenberg et al., 2006, 2013), domestic animal (Ratcliffe et al., 2010), food waste (Grémillet et al.,
370 2008) and marine pollution (Trathan et al., 2015) on seabirds. Studies with similar conditions to our
371 study (i.e. seabird in parks or area without tourists due to lock-downs) found that the absence of
372 tourists could, counter-intuitively, lead to more disturbance for the seabirds, which translated in a
373 later laying date and more egg predation (Hentati-Sundberg et al., 2021), underlining the protective
374 role tourists can have for some species. We did not find such an effect in the parameters studied in
375 this paper. Here, we found no effects of the presence of tourists on little penguins activities.

376 Still, little penguins are known to be sensitive to anthropogenic activities like human
377 presence around the nest (Colombelli-Négrel & Katsis, 2021). A recent study identified the negative
378 effect of anthropogenic activities, *i.e.* white light sources, at night on little penguins (Costello &
379 Colombelli-Négrel, 2023), but evidences are mixed since other study find the opposite (Rodríguez
380 et al., 2018). Multiple hypotheses could explain the absence of response during the anthropause in
381 our study. One could argue that the duration and/or magnitude of the anthropause was negligible to
382 trigger a response in the foraging behavior of little penguins. Plasticity being species dependent
383 (Crawford et al., 2017), more studies on little penguins would be necessary to assess the extent of
384 their plasticity in response to anthropogenic activities, and the potential different threshold that
385 could trigger a response in the studied parameters (Cairns, 1988). On land, predators of little
386 penguins are mainly goannas, snakes and cats (Colombelli-Négrel & Katsis, 2021). However, these
387 predators are a not a thread at Phillip Island, thanks to a successful conservation program in place,
388 with a well managed tourists' pressure (BirdLife International, 2023; Rodríguez et al., 2018).
389 Long-term exposition to tourists at the Penguin Parade ®, little penguins could have habituated to
390 anthropogenic disturbance (Rodríguez et al., 2016; Viblanc et al., 2012). Therefore it could mean
391 that the predation and disturbance pressure on-land were unchanged during the lock-downs. Finally,
392 the absence of shifts on little penguins trophic niche in 2020 suggests that even if the marine
393 benefited from the lock-down, improving food availability, we did not detected any changes in the
394 diet of little penguins.

395 To our knowledge, this paper provides the first empirical assessment of the negative effect
396 of marine traffic on little penguins' foraging behavior during their breeding period. Our study
397 underlines that the at-sea disturbances are more important than the on-land ones when it comes to
398 affect little penguins foraging. The lock-downs did not trigger a reduction of the marine traffic in
399 the Bass Strait but thanks to a long-term data set, we were able to asses the effect of marine traffic
400 on little penguins foraging. As expected, we found a negative effect of marine traffic intensity on
401 little penguins foraging efficiency but not on their spatial distribution.

402 Our spatial analysis revealed an overlap between little penguins and marine traffic in the
403 Bass strait. However, in the Bass strait, fisheries represent only a small proportion (< 1 %) of the
404 marine traffic in comparison with cargo (50-60 %), tanker (10-20 %), and passenger vessels (5-8 %
405 supplementary figure 1). It is therefore unlikely that the observed effect is due to a competition with
406 fisheries for food. Marine traffic can cause other indirect disturbance, through avoidance behaviour
407 of predators (Jarrett et al., 2021; Pichegru et al., 2022) and preys (Ivanova et al., 2020), or
408 environmental pollution. More investigations is needed on the mechanism to fully understand how
409 marine traffic impacts little penguins to be implemented on marine spatial planning.

410 Using quantitative information about human activity, like the number of tourists, rather than
411 qualitative one (e. g. comparing lock-down season vs past observed trends) is key to compare study
412 results and assess the shape of the response of wildlife to anthropogenic activities. Indeed, many
413 studies fail to properly quantify anthropogenic activities, and only compared “COVID years” with
414 other years before and/or after (Gordo et al., 2021; Hentati-Sundberg et al., 2021; Sala et al., 2021).
415 While informative, this approach does not allow to properly disentangle anthropogenic pressure
416 from seasonal and environmental variations. Incorporating a quantification of anthropogenic
417 pressure in our models (i.e. number of tourists and vessels) allowed us to disentangle the natural
418 inter- and intra-annual variations from anthropogenic pressure. Our study highlighted that long-term
419 monitoring studies are key to be able to disentangle such effects.

420 The effect of the anthropauses caused by the COVID related lock-downs on little penguins’
421 ecology during the breeding might be negligible compared to the ones induced by long-term
422 environmental variations and global changes (Joly et al., 2022). Other significant effects found in
423 our study are mostly related to intra and inter-annual variations. Thanks to long-term monitoring
424 and online data availability, we were able to have a detailed picture of the impact of anthropogenic
425 activities over the 10 years period. Species showing high plasticity and therefore quickly responding
426 to reduced pressures during anthropauses are likely to use that same plasticity in the other way
427 when anthropogenic activities increase again. Such punctual changes could be buffered by

428 phenotypic plasticity and unlikely to change population trends compared to long-term variations
429 (Gordo et al., 2021).

430 In conclusion, we did not detected any positive or negative effect of COVID-19 lock-downs
431 on the little penguin breeding ecology, despite of our robust dataset used in the analysis. We did
432 show that behavioral variations during their breeding cycle of little penguins of the Phillip Island
433 Nature Park was mostly due to the inter- and intra-annual variation. We revealed that anthropogenic
434 effect due to increased marine traffic can affect foraging efficiency of little penguins. Still, as
435 seabirds live at the interface between sea and land, more information needs to be gathered on the
436 mechanisms behind the effect of marine activity on little penguins foraging and on the effect of on-
437 land anthropogenic activity on little penguins breeding. Better understanding these sources of
438 pressure could help the efficient implementation of marine spatial planning and validate the
439 efficiency of mitigation measures occurring in natural parks. Given the important specific and
440 spatial variability in the responses to anthropogenic activities, the fast change of the marine
441 environment in this region, maintaining and developing long-term monitoring sites and studies is
442 key to guide conservation policies. This will help researchers to better distinguish between
443 environmental and anthropogenic effects on wild species.

444 **Authors contributions**

445 Conceptualization : AC, YRC, AK

446 Data curation : BD, MC, NJ, AK

447 Analysis : BD

448 Writing : BD, MC

449 Review of draft : all authors

450 Supervision : MC, AK, AC

451 **Acknowledgements**

452 We thank Phillip Island Nature Parks for their continued support and commitment to penguin
453 research. We thank all the students and volunteers for their tireless support in collecting these data
454 over the years, particularly the Nature Parks's research technical staff Leanne Renwick, Paula
455 Wasiak, Meagan Tucker, Marjolein van Polanen Petel and Jordan Roberts. We thank all the
456 students and volunteers for their tireless support in collecting these data. Field work protocol was
457 approved by the ethics committee of the Phillip Island Nature Park Animal Experimentation
458 Committee with a research permit issued by the Department of Environment, Land, Water and
459 Planning of Victoria, Australia.

460 **Conflict of interest**

461 The authors declare no conflicts of interest.

462 **Data availability statement**

463 Sample dataset and all R codes used to manipulate and analyze the data used are available at
464 <https://github.com/bendps/COVIDxLP>.

465 **Funding**

466 The long-term data set received several funding sources over the years: the Penguin Foundation,
467 Australian Academy of Science, Australian Research Council, Australian Antarctic Division, Kean
468 Electronics, ATT Kings, and Japan Society for the Promotion of Science. This project has received
469 funding from the European Union's Horizon 2020 research and innovation programme under the

470 Marie Sklodowska-Curie grant agreement No 890284, "Modelling Foraging Fitness in Marine
471 predators (MuFFIN)", awarded to Marianna Chimienti.

472

473 References

- Barreau, E., Kato, A., Chiaradia, A., & Ropert-Coudert, Y. (2021). The consequences of chaos: Foraging activity of a marine predator remains impacted several days after the end of a storm. *PLOS ONE*, 16(7), e0254269. <https://doi.org/10.1371/journal.pone.0254269>
- , Bates, A. E., Primack, R. B., Biggar, B. S., Bird, T. J., Clinton, M. E., Command, R. J., Richards, C., Shellard, M., Geraldi, N. R., Vergara, V., Acevedo-Charry, O., Colón-Piñeiro, Z., Ocampo, D., Ocampo-Peñuela, N., Sánchez-Clavijo, L. M., Adamescu, C. M., Cheval, S., Racoviceanu, T., Adams, M. D., ... Duarte, C. M. (2021). Global COVID-19 lockdown highlights humans as both threats and custodians of the environment. *Biological Conservation*, 263, 109175. <https://doi.org/10.1016/j.biocon.2021.109175>
- , BirdLife International. (2023). Species factsheet: *Eudyptula minor*. Downloaded from <http://datazone.birdlife.org/species/factsheet/little-penguin-eudyptula-minor> on 30/06/2023
- , Bost, C.-A., Jaeger, A., Huin, W., Koubbi, P., Halsey, L., Hanuise, N., & Handrich, Y. (2008). Monitoring prey availability via data loggers deployed on seabirds: advances and present limitations. *Fisheries for Global Welfare and Environment Memorial Book of the 5th World Fisheries Congress*, 121–137.
- , Bozdogan, H. (1987). Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. *Psychometrika*, 52(3), 345–370. <https://doi.org/10.1007/BF02294361>
- , Cairns, D. K. (1988). Seabirds as Indicators of Marine Food Supplies. *Biological Oceanography*, 5(4), 261–271. <https://doi.org/10.1080/01965581.1987.10749517>
- , Calenge, C. (2006). The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 1035.
- , Cannell, B. L., Campbell, K., Fitzgerald, L., Lewis, J. A., Baran, I. J., & Stephens, N. S. (2016). Anthropogenic trauma is the most prevalent cause of mortality in Little Penguins, *Eudyptula minor*, in Perth, Western Australia. *Emu - Austral Ornithology*, 116(1), 52–61.

<https://doi.org/10.1071/MU15039>

, Cannell, B. L., & Cullen, J. M. (1998). The foraging behaviour of Little Penguins *Eudyptula minor* at different light levels. *Ibis*, 140(3), 467–471. <https://doi.org/10.1111/j.1474-919X.1998.tb04608.x>

, Cannell, B. L., Ropert-Coudert, Y., Radford, B., & Kato, A. (2020). The diving behaviour of little penguins in Western Australia predisposes them to risk of injury by watercraft. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(3), 461–474.

<https://doi.org/10.1002/aqc.3272>

, Catry, T., Lourenço, P. M., Lopes, R. J., Carneiro, C., Alves, J. A., Costa, J., Rguibi-Idrissi, H., Bearhop, S., Piersma, T., & Granadeiro, J. P. (2016). Structure and functioning of intertidal food webs along an avian flyway: a comparative approach using stable isotopes. *Functional Ecology*, 30(3), 468–478. <https://doi.org/10.1111/1365-2435.12506>

, Chiaradia, A., & Kerry, K. R. (1999). Daily Nest Attendance and Breeding Performance in the Little Penguin *Eudyptula Minor* at Phillip Island, Australia. 8.

, Chiaradia, A., McBride, J., Murray, T., & Dann, P. (2007). Effect of fog on the arrival time of little penguins *Eudyptula minor*: a clue for visual orientation? *Journal of Ornithology*, 148(2), 229–233. <https://doi.org/10.1007/s10336-007-0125-5>

, Chiaradia, A., Ramírez, F., Forero, M. G., & Hobson, K. A. (2016). Stable Isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) Combined with Conventional Dietary Approaches Reveal Plasticity in Central-Place Foraging Behavior of Little Penguins *Eudyptula minor*. *Frontiers in Ecology and Evolution*, 3, 154.

<https://doi.org/10.3389/fevo.2015.00154>

, Collins, M., Cullen, J. M., & Dann, P. (1999). Seasonal and annual foraging movements of little penguins from Phillip Island, Victoria. *Wildlife Research*, 26(6), 705–721.

<https://doi.org/10.1071/wr98003>

, Colombelli-Négre, D., & Katsis, A. C. (2021). Little penguins are more aggressive on islands that experience greater unregulated human disturbance. *Animal Behaviour*, 182, 195–202.

<https://doi.org/10.1016/j.anbehav.2021.10.012>

, Costello, E. C., & Colombelli-Négre, D. (2023). Human activities at night negatively impact Little Penguin (*Eudyptula minor*) numbers and behaviours. *Ibis*, *ibi.13217*.

<https://doi.org/10.1111/ibi.13217>

, Crawford, R., Ellenberg, U., Frere, E., Hagen, C., Baird, K., Brewin, P., Crofts, S., Glass, J., Mattern, T., Pompert, J., Ross, K., Kemper, J., Ludynia, K., Sherley, R. B., Steinfurth, A., Suazo, C. G., Yorio, P., Tamini, L., Mangel, J. C., ... Small, C. (2017). Tangled and drowned: a global review of penguin bycatch in fisheries. *Endangered Species Research*, *34*, 373–396.

<https://doi.org/10.3354/esr00869>

, Dann, P., & Chambers, L. (2013). Ecological effects of climate change on little penguins *Eudyptula minor* and the potential economic impact on tourism. *Climate Research*, *58*(1), 67–79.

<https://doi.org/10.3354/cr01187>

, Duhem, C., Roche, P., Vidal, E., & Tatoni, T. (2008). Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. *Population Ecology*, *50*(1), 91–100.

<https://doi.org/10.1007/s10144-007-0059-z>

, Durant JM, Hjermmann DØ, Frederiksen M, Charrassin JB, Le Maho Y, Sabarros PS, Crawford RJM, & Stenseth NC. (2009). Pros and cons of using seabirds as ecological indicators. *Climate Research*, *39*(2), 115–129. <https://www.int-res.com/abstracts/cr/v39/n2/p115-129/>

, Einoder, L. D. (2009). A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research*, *95*(1), 6–13. <https://doi.org/10.1016/j.fishres.2008.09.024>

, Ellenberg, U., Mattern, T., & Seddon, P. J. (2013). Heart rate responses provide an objective evaluation of human disturbance stimuli in breeding birds. *Conservation Physiology*, *1*(1), cot013–cot013. <https://doi.org/10.1093/conphys/cot013>

, Ellenberg, U., Mattern, T., Seddon, P. J., & Jorquera, G. L. (2006). Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. *Biological Conservation*, *133*(1), 95–106.

<https://doi.org/10.1016/j.biocon.2006.05.019>

, Ellenberg, U., Setiawan, A. N., Cree, A., Houston, D. M., & Seddon, P. J. (2007). Elevated hormonal stress response and reduced reproductive output in Yellow-eyed penguins exposed to unregulated tourism. *General and Comparative Endocrinology*, 152(1), 54–63.

<https://doi.org/10.1016/j.ygcen.2007.02.022>

, Everard, M. (2020). Managing socio-ecological systems: who, what and how much? The case of the Banas river, Rajasthan, India. *Current Opinion in Environmental Sustainability*, 44, 16–25.

<https://doi.org/10.1016/j.cosust.2020.03.004>

, Fieberg, J., & Kochanny, C. O. (2005). Quantifying Home-Range Overlap: The Importance of the Utilization Distribution. *The Journal of Wildlife Management*, 69(4), 1346–1359.

[https://doi.org/10.2193/0022-541X\(2005\)69\[1346:QHOTIO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2)

, French, R. K., Muller, C. G., Chilvers, B. L., & Battley, P. F. (2019). Behavioural consequences of human disturbance on subantarctic Yellow-eyed Penguins *Megadyptes antipodes*. *Bird Conservation International*, 29(2), 277–290. <https://doi.org/10.1017/S0959270918000096>

, Furness, R. W., & Camphuysen, K. (C. J.). (1997). Seabirds as monitors of the marine environment. *ICES Journal of Marine Science*, 54(4), 726–737.

<https://doi.org/10.1006/jmsc.1997.0243>

, Gordo, O., Brotons, L., Herrando, S., & Gargallo, G. (2021). Rapid behavioural response of urban birds to COVID-19 lockdown. *Proceedings of the Royal Society B: Biological Sciences*, 288(1946), 20202513. <https://doi.org/10.1098/rspb.2020.2513>

, Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A. G., Wilkinson, S., Crawford, R. J. M., & Ryan, P. G. (2008). A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society B: Biological Sciences*, 275(1639), 1149–1156.

<https://doi.org/10.1098/rspb.2007.1763>

, Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., Scales, K. L., Sydeman, W. J., & Bograd, S. J. (2019). Marine top predators as climate and ecosystem sentinels.

Frontiers in Ecology and the Environment, 17(10), 565–574. <https://doi.org/10.1002/fee.2125>

, Hentati-Sundberg, J., Berglund, P.-A., Hejdström, A., & Olsson, O. (2021). COVID-19 lockdown reveals tourists as seabird guardians. *Biological Conservation*, 254, 108950.

<https://doi.org/10.1016/j.biocon.2021.108950>

, Hijmans, R. J. (2022). raster: Geographic Data Analysis and Modeling. <https://rspatial.org/raster>

, Hobson, K. A., Piatt, J. F., & Pitocchelli, J. (1994). Using Stable Isotopes to Determine Seabird Trophic Relationships. *Journal of Animal Ecology*, 63(4), 786–798. <https://doi.org/10.2307/5256>

, Holles, S., Simpson, S. D., Radford, A. N., Berten, L., & Lecchini, D. (2013). Boat noise disrupts orientation behaviour in a coral reef fish. *Marine Ecology Progress Series*, 485, 295–300.

<https://doi.org/10.3354/meps10346>

, Ivanova, S., Kessel, S. T., Espinoza, M., McLean, M. F., O’Neill, C., Landry, J., Hussey, N. E., Williams, R., Vagle, S., & Fisk, A. T. (2020). Shipping alters the movement and behavior of Arctic cod (*Boreogadus saida*), a keystone fish in Arctic marine ecosystems. *Ecological Applications*.

<https://doi.org/10.1002/eap.2050>

, Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80(3), 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>

, Jarrett, D., Calladine, J., Cook, A. S. C. P., Upton, A., Williams, J., Williams, S., Wilson, J. M., Wilson, M. W., Woodward, I., & Humphreys, E. M. (2021). Behavioural responses of non-breeding waterbirds to marine traffic in the near-shore environment. *Bird Study*, 68(4), 443–454.

<https://doi.org/10.1080/00063657.2022.2113855>

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

, Kadykalo, A. N., Beaudoin, C., Hackenburg, D. M., Young, N., & Cooke, S. J. (2022). Social–ecological systems approaches are essential for understanding and responding to the complex

impacts of COVID-19 on people and the environment. *PLOS Sustainability and Transformation*, 1(4), e0000006. <https://doi.org/10.1371/journal.pstr.0000006>

, Kato, A., Ropert-Coudert, Y., & Chiaradia, A. (2008). Regulation of Trip Duration by an Inshore Forager, the Little Penguin (*Eudyptula Minor*), During Incubation. *The Auk*, 125(3), 588–593. <https://doi.org/10.1525/auk.2008.06273>

, Klomp, N. I., & Wooller, R. D. (1991). Patterns of Arrival and Departure by Breeding Little Penguins at Penguin Island, Western Australia. *Emu*, 91(1), 32–35. <https://doi.org/10.1071/mu9910032>

, Lamers, M., & Student, J. (2021). Learning from COVID-19? An environmental mobilities and flows perspective on dynamic vulnerabilities in coastal tourism settings. *Maritime Studies*. <https://doi.org/10.1007/s40152-021-00242-1>

, Mace, G. M. (2014). Whose conservation? *Science*, 345(6204), 1558–1560. <https://doi.org/10.1126/science.1254704>

, Manenti, R., Mori, E., Di Canio, V., Mercurio, S., Picone, M., Caffi, M., Brambilla, M., Ficetola, G. F., & Rubolini, D. (2020). The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. *Biological Conservation*, 249, 108728. <https://doi.org/10.1016/j.biocon.2020.108728>

, Margalida, A., Colomer, M. À., & Oro, D. (2014). Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. *Ecological Applications*, 24(3), 436–444. <https://doi.org/10.1890/13-0414.1>

, Mattern, T., Ellenberg, U., Houston, D. M., Lamare, M., Davis, L. S., Hezik, Y. van, & Seddon, P. J. (2013). Straight Line Foraging in Yellow-Eyed Penguins: New Insights into Cascading Fisheries Effects and Orientation Capabilities of Marine Predators. *PLOS ONE*, 8(12), e84381. <https://doi.org/10.1371/journal.pone.0084381>

, McClintock, B. T., & Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*, 9(6), 1518–1530.

<https://doi.org/10.1111/2041-210X.12995>

, Pelletier, L., Chiaradia, A., Kato, A., & Ropert-Coudert, Y. (2014). Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia*.

<https://doi.org/10.1007/s00442-014-3018-3>

, Piatt, J. F., Harding, A. M. A., Shultz, M. T., Speckman, S. G., van Pelt, T. I., Drew, G. S., & Kettle, A. B. (2007). Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, 352, 221–234. USGS Publications Warehouse.

<https://doi.org/10.3354/meps07078>

, Piatt, J. F., Sydeman, W. J., & Wiese, F. (2007). Introduction: a modern role for seabirds as indicators. *Marine Ecology Progress Series*, 352, 199–204. <https://www.int-res.com/abstracts/meps/v352/p199-204/>

, Pichegru, L., Grémillet, D., Crawford, R. J. M., & Ryan, P. G. (2010). Marine no-take zone rapidly benefits endangered penguin. *Biology Letters*. <https://doi.org/10.1098/rsbl.2009.0913>

, Pichegru, L., Nyengera, R., McInnes, A. M., & Pistorius, P. (2017). Avoidance of seismic survey activities by penguins. *Scientific Reports*, 7(1), 16305. <https://doi.org/10.1038/s41598-017-16569-x>

, Pichegru, L., Vibert, L., Thiebault, A., Charrier, I., Stander, N., Ludynia, K., Lewis, M., Carpenter-Kling, T., & McInnes, A. (2022). Maritime traffic trends around the southern tip of Africa – Did marine noise pollution contribute to the local penguins' collapse? *Science of The Total Environment*, 849, 157878. <https://doi.org/10.1016/j.scitotenv.2022.157878>

, Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2021). nlme: Linear and Nonlinear Mixed Effects Models. <https://CRAN.R-project.org/package=nlme>

, Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montaña, C. G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, 152(1), 179–189. <https://doi.org/10.1007/s00442-006-0630-x>

, Poupart, T. A., Waugh, S. M., Bost, C., Bost, C.-A., Dennis, T., Lane, R., Rogers, K., Sugishita, J., Taylor, G. A., Wilson, K.-J., Zhang, J., & Arnould, J. P. Y. (2017). Variability in the foraging

range of *Eudyptula minor* across breeding sites in central New Zealand. *New Zealand Journal of Zoology*, 44(3), 225–244. <https://doi.org/10.1080/03014223.2017.1302970>

, R Core Team. (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.R-project.org/>

, Ramírez, F., Afán, I., Davis, L. S., & Chiaradia, A. (2017). Climate impacts on global hot spots of marine biodiversity. *Science Advances*, 3(2), e1601198. <https://doi.org/10.1126/sciadv.1601198>

, Ramírez, F., Forero, M. G., Hobson, K. A., & Chiaradia, A. (2015). Older female little penguins *Eudyptula minor* adjust nutrient allocations to both eggs. *Journal of Experimental Marine Biology and Ecology*, 468, 91–96. <https://doi.org/10.1016/j.jembe.2015.03.020>

, Ratcliffe, N., Bell, M., Pelembe, T., Boyle, D., Benjamin, R., White, R., Godley, B., Stevenson, J., & Sanders, S. (2010). The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. *Oryx*, 44(01), 20–29. <https://doi.org/10.1017/S003060530999069X>

, Rodríguez, A., Chiaradia, A., Wasiak, P., Renwick, L., & Dann, P. (2016). Waddling on the Dark Side: Ambient Light Affects Attendance Behavior of Little Penguins. *Journal of Biological Rhythms*, 31(2), 194–204. <https://doi.org/10.1177/0748730415626010>

, Rodríguez, A., Holmberg, R., Dann, P., & Chiaradia, A. (2018). Penguin colony attendance under artificial lights for ecotourism. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329(8–9), 457–464. <https://doi.org/10.1002/jez.2155>

, Rutz, C., Loretto, M.-C., Bates, A. E., Davidson, S. C., Duarte, C. M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R. B., Ropert-Coudert, Y., Tucker, M. A., Wikelski, M., & Cagnacci, F. (2020). COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. *Nature Ecology & Evolution*, 4(9), 1156–1159. <https://doi.org/10.1038/s41559-020-1237-z>

, Sala, M. M., Peters, F., Sebastián, M., Cardelús, C., Calvo, E., Marrasé, C., Massana, R., Pelejero, C., Sala-Coromina, J., Vaqué, D., & Gasol, J. M. (2021). COVID-19 lockdown moderately increased oligotrophy at a marine coastal site. *Science of The Total Environment*, 151443.

<https://doi.org/10.1016/j.scitotenv.2021.151443>

, Salton, M., Saraux, C., Dann, P., & Chiaradia, A. (2015). Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. *Royal Society Open Science*.

<https://doi.org/10.1098/rsos.140390>

, Sánchez, S., Reina, R. D., Kato, A., Ropert-Coudert, Y., Cavallo, C., Hays, G. C., & Chiaradia, A. (2018). Within-colony spatial segregation leads to foraging behaviour variation in a seabird. *Marine Ecology Progress Series*, 606, 215–230. <https://doi.org/10.3354/meps12764>

, Saraux, C., Chiaradia, A., Maho, Y., & Ropert-Coudert, Y. (2011). Everybody needs somebody: unequal parental effort in little penguins. <https://doi.org/10.1093/BEHECO/ARR049>

, Seaman, D. E., Griffith, B., & Powell, R. A. (1998). KERNELHR: A program for estimating animal home ranges. *Wildlife Society Bulletin*, 26(1), 95–100. USGS Publications Warehouse. <http://pubs.er.usgs.gov/publication/1015784>

, Siddig, A. A. H., Ellison, A. M., Ochs, A., Villar-Leeman, C., & Lau, M. K. (2016). How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in *Ecological Indicators*. *Ecological Indicators*, 60, 223–230.

<https://doi.org/10.1016/j.ecolind.2015.06.036>

, Sugihara, G., May, R., Ye, H., Hsieh, C., Deyle, E., Fogarty, M., & Munch, S. (2012). Detecting Causality in Complex Ecosystems. *Science*, 338(6106), 496–500.

<https://doi.org/10.1126/science.1227079>

, Sutherland, D. R., & Dann, P. (2014). Population trends in a substantial colony of Little Penguins: three independent measures over three decades. *Biodiversity and Conservation*, 23(1), 241–250.

<https://doi.org/10.1007/s10531-013-0597-y>

, Trathan, P. N., García-Borboroglu, P., Boersma, D., Bost, C., Crawford, R. J. M., Crossin, G. T., Cuthbert, R. J., Dann, P., Davis, L. S., De La Puente, S., Ellenberg, U., Lynch, H. J., Mattern, T., Pütz, K., Seddon, P. J., Trivelpiece, W., & Wienecke, B. (2015). Pollution, habitat loss, fishing, and climate change as critical threats to penguins. *Conservation Biology*, 29(1), 31–41.

<https://doi.org/10.1111/cobi.12349>

, Tucker, M. A., Alexandrou, O., Bierregaard Jr., R. O., Bildstein, K. L., Böhning-Gaese, K., Bracis, C., Brzorad, J. N., Buechley, E. R., Cabot, D., Calabrese, J. M., Carrapato, C., Chiaradia, A., Davenport, L. C., Davidson, S. C., Desholm, M., DeSorbo, C. R., Domenech, R., Enggist, P., Fagan, W. F., ... Mueller, T. (2019). Large birds travel farther in homogeneous environments. *Global Ecology and Biogeography*, 28(5), 576–587. <https://doi.org/10.1111/geb.12875>

Global Ecology and Biogeography, 28(5), 576–587. <https://doi.org/10.1111/geb.12875>

, Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., ... Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359(6374), 466–469. <https://doi.org/10.1126/science.aam9712>

, Viblanc, V. A., Smith, A. D., Gineste, B., & Groscolas, R. (2012). Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC Ecology*, 12(1), 10. <https://doi.org/10.1186/1472-6785-12-10>

, Watanuki, Y., Wanless, S., Harris, M., Lovvorn, J. R., Miyazaki, M., Tanaka, H., & Sato, K. (2006). Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. *Journal of Experimental Biology*, 209(7), 1217–1230. <https://doi.org/10.1242/jeb.02128>

, Wei, Y., Wu, S., & Tesemma, Z. (2018). Re-orienting technological development for a more sustainable human–environmental relationship. *Current Opinion in Environmental Sustainability*, 33, 151–160. <https://doi.org/10.1016/j.cosust.2018.05.022>

, Wilson, R. P., Pütz, K., Peters, G., Culik, B., Scolaro, J. A., Charrassin, J.-B., & Ropert-Coudert, Y. (1997). Long-Term Attachment of Transmitting and Recording Devices to Penguins and Other Seabirds. *Wildlife Society Bulletin (1973-2006)*, 25(1), 101–106.

<https://www.jstor.org/stable/3783290>

1 **Figures**

2 **Figure 1:** Evolution of anthropogenic activities in the studied area. (A) Daily number of tourists
3 at the penguin parade ® between 2010 and 2020. (B) Daily number of vessels at sea in the
4 foraging area of little penguins between 2014 and 2020. Astariscs represent statistical
5 significance of post-hoc comparisons between 2020 (lock-down season) and the others (2010-
6 2019, ** = $p < 0.01$, *** = $p < 0.001$).

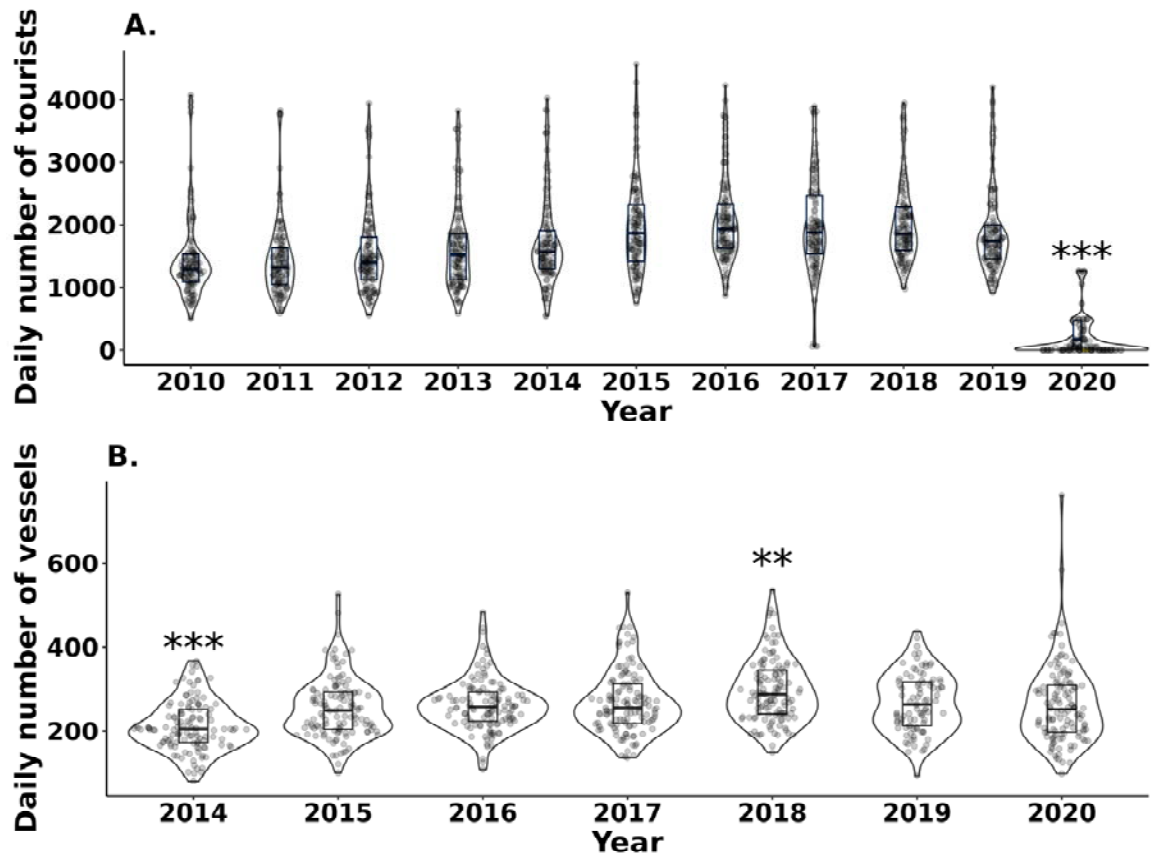


Figure 2: Spatial distribution of little penguins and marine traffic between 2014 and 2020. The black dot represents the studied colony in Phillip Island.

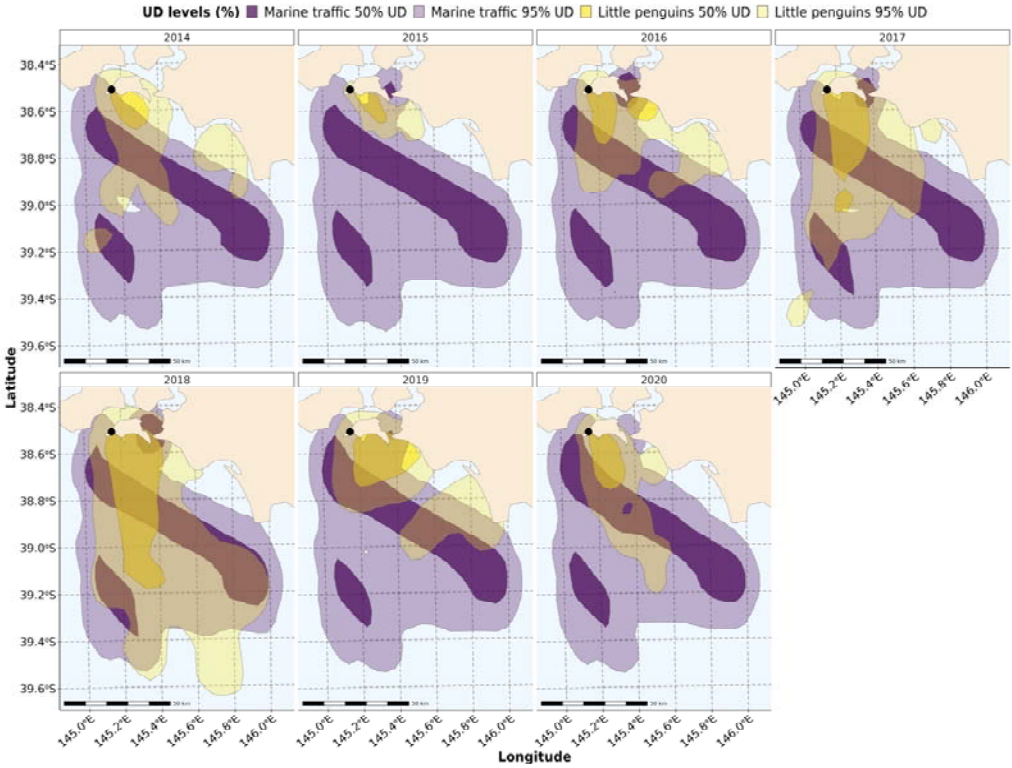


Figure 3: Anthropogenic activities effect on APMS-derived parameters. (A) Departure time relatively to nautical dawn, and (B) Arrival time relatively to nautical dusk of little penguins at the colony depending on the number of tourists. Effect of the number of vessels on the (C) Mass gain per day at sea and (D) Meal mass given to the chicks at the colony. Colored points represent a season average, and white points the overall mean with its SE. Dashed lines represent the 95% CI around model predictions.

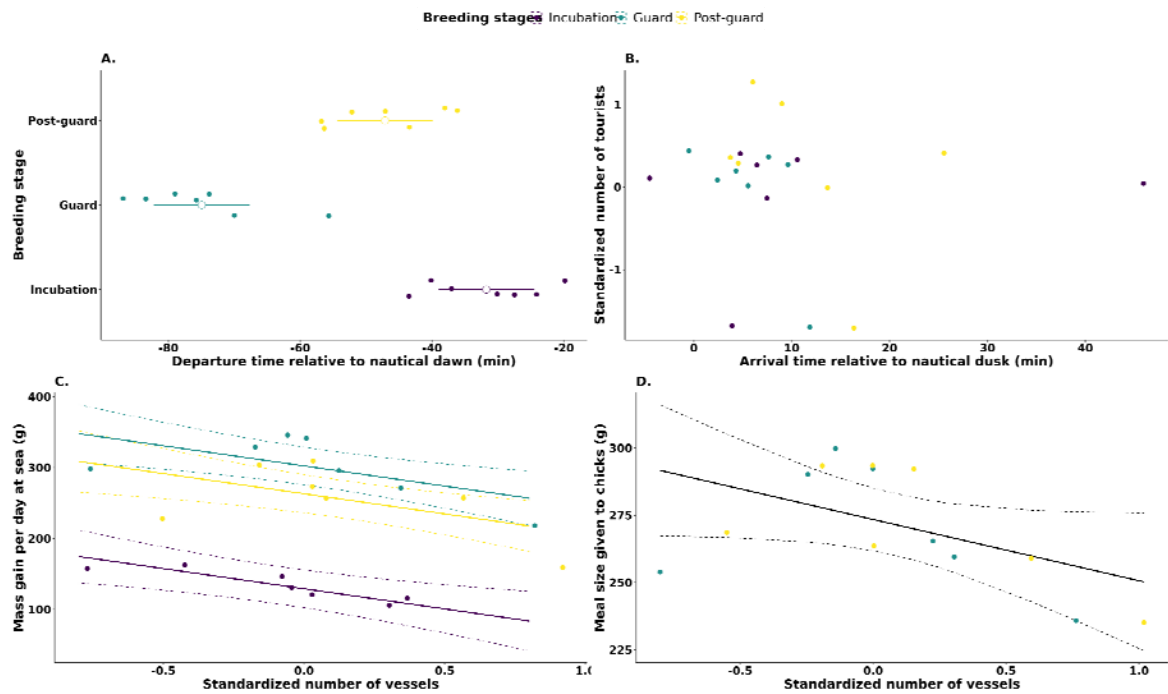


Figure 4: Isotopic niche of little penguins between 2010 and 2020, across different breeding stages. Ellipses represent the corrected standard ellipses of each niche (40% of the individuals).

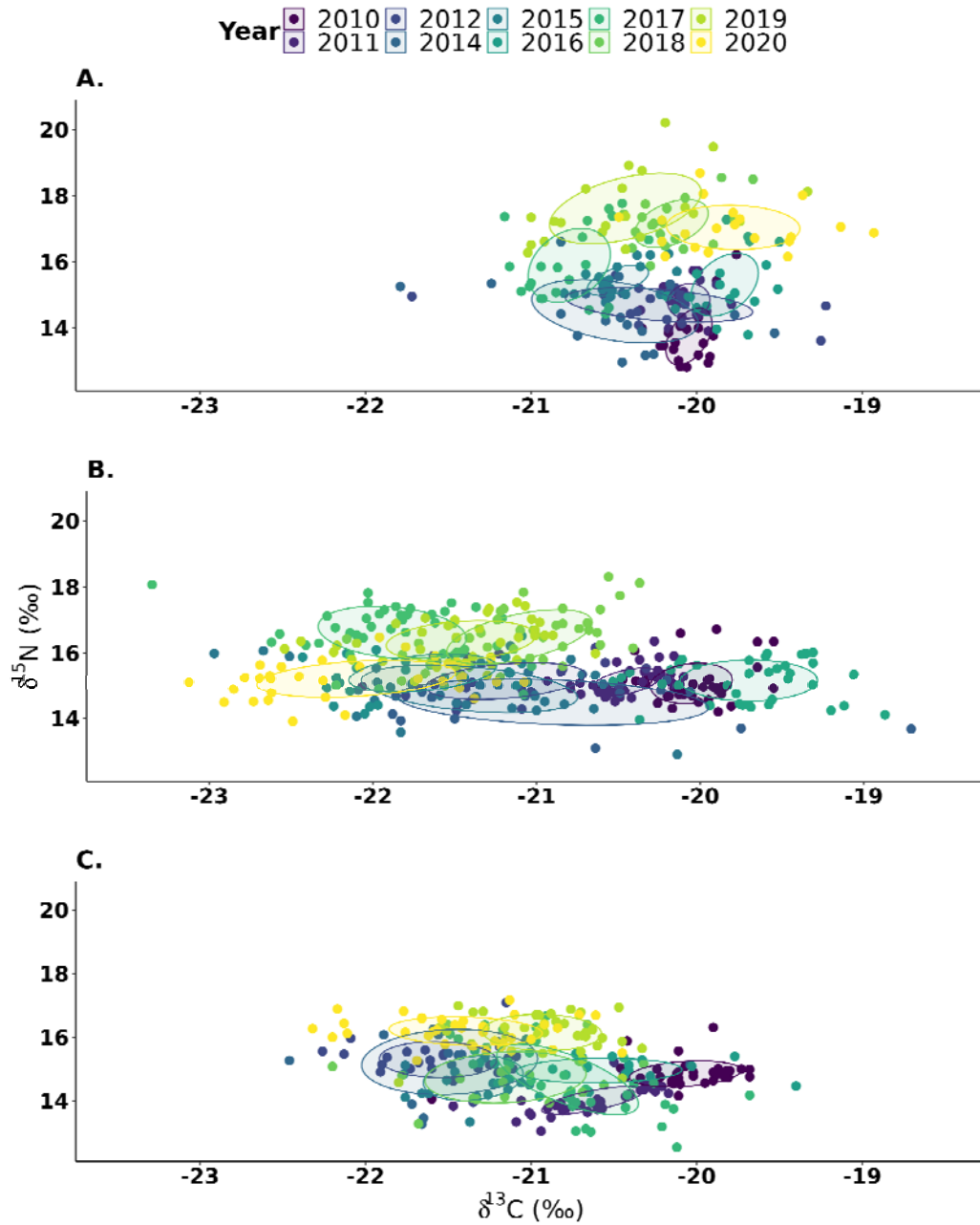
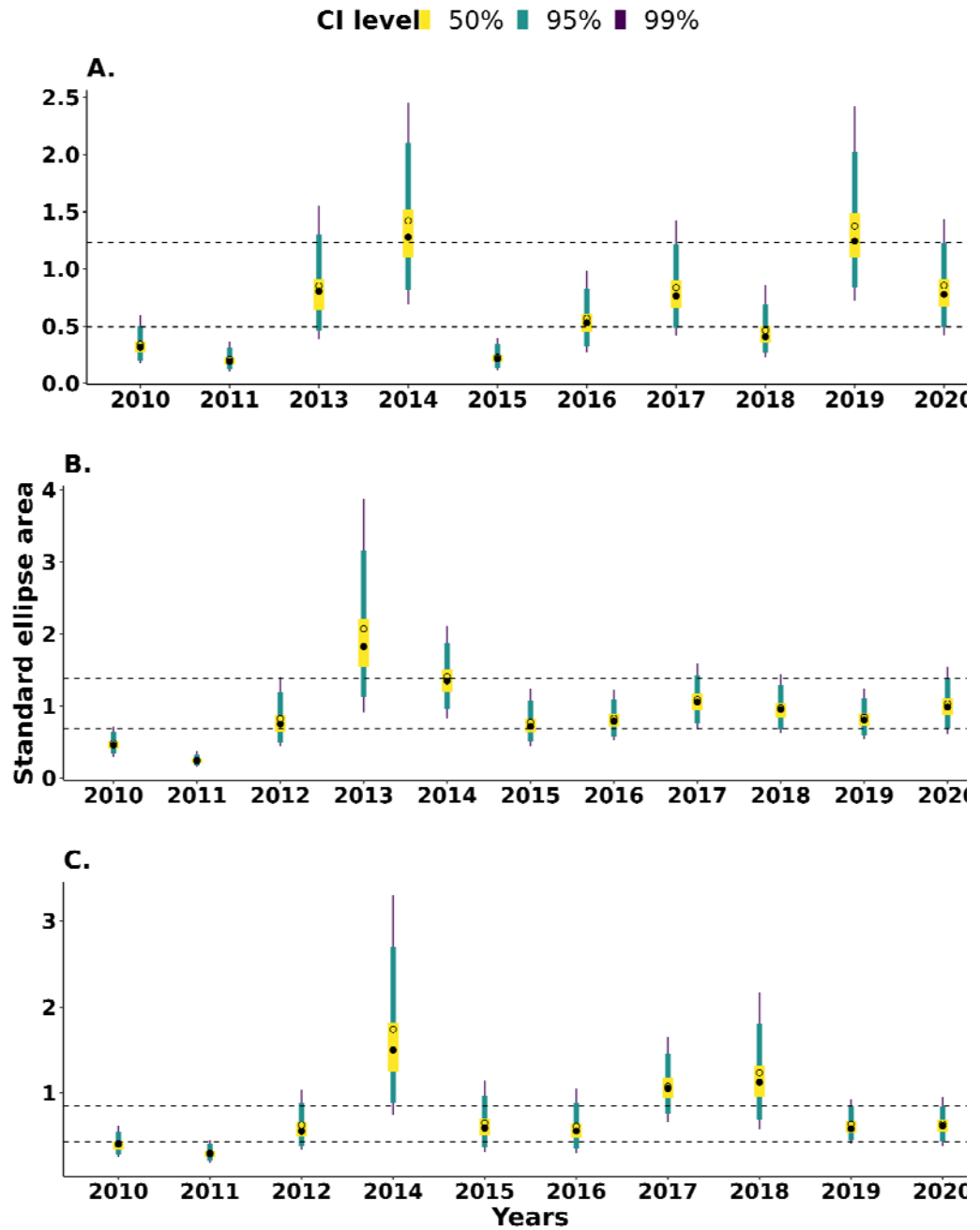


Figure 5: Standard ellipses' area of little penguin's isotopic niches between 2010 and 2020 during different breeding stages. Black dots represent the mode of the Bayesian standard ellipse area, and error bars the confidence intervals at 50, 95 and 99%. Circles represent the corrected standard ellipse areas.



Tables

8 Table 1. Number of little penguins and type of loggers deployed for each year and breeding
 9 stage. (Females/Males)

10

		Season										
		2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Breeding stage	Incubation	0	16 (5/1)	16 (8/8)	9 (5/4)	26 (12/14)	23 (7/16)	21 (12/9)	28 (20/8)	30 (14/16)	24 (10/14)	15 (8/7)
	Guard	28 (13/15)	18 (10/8)	9 (4/5)	10 (5/5)	19 (9/10)	16 (9/7)	13 (5/8)	13 (7/6)	17 (7/10)	17 (8/9)	18 (10/8)
	Post-guard	7 (3/4)	19 (12/7)	16 (9/7)	4 (4/0)	12 (7/5)	11 (6/5)	12 (7/5)	19 (12/7)	16 (8/8)	9 (2/7)	12 (9/3)
Logger type								CatTrack and AxyTrek	CatTrack		AxyTrek	

11

12

13

14