

1 **Title**

2 Juvenile emperor penguin range calls for extended conservation measures in the Southern Ocean

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## 21 **Abstract**

22 To protect the unique Southern Ocean biodiversity, conservation measures like marine protected  
23 areas (MPAs) are implemented based on the known habitat distribution of ecologically important  
24 species. However, distribution models focus on adults, neglecting that immatures animals can inhabit  
25 vastly different areas. Here, we show that current conservation efforts in the Southern Ocean are  
26 insufficient for ensuring the protection of the highly mobile Emperor penguin. We find that juveniles  
27 spend ~90% of their time outside the boundaries of proposed and existing MPAs, and that their  
28 distribution extends far beyond (> 1500 km) the species' extent of occurrence as defined by the  
29 International Union for Conservation of Nature. We argue that strategic conservation plans for  
30 Emperor penguin and long-lived ecologically important species must consider the dynamic habitat  
31 range of all age classes.

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## 42 Introduction

43 Anthropogenic environmental changes lead to upheaval even in remote and apparently untouched  
44 ecosystems such as the Antarctic and the Southern Ocean. Marine top predators, such as seabirds  
45 and marine mammals, play a pivotal role in marine ecosystems <sup>1</sup>, and any disruptions in their  
46 abundance and distribution can have a major impact on the functioning and resilience of ecosystems  
47 <sup>2</sup>. At the same time, top predators are indicators of ecosystem health because of their high position  
48 in the trophic cascade and the vast, ocean basin-scale habitat of individual animals <sup>3,4</sup>. Thus, top  
49 predators integrate signals from across the food web and are therefore important bioindicators <sup>5</sup>.  
50 The health, abundance and distribution of marine top predators are consequently key metrics in  
51 ecosystem-based management and systematic conservation planning <sup>6</sup>.

52 Effective conservation plans require comprehensive consideration of the at-sea distribution of  
53 species, including each life-history stage such as juveniles and immatures as they constitute an  
54 essential part of the total population <sup>7</sup>. However, in some of these taxa, in particular in many seabird  
55 species, the distribution of juveniles and immatures is difficult to assess and is therefore often  
56 neglected. This is especially true for polar ecosystems, where remoteness and the extreme  
57 environmental conditions hamper data collection.

58 Currently, the Southern Ocean experiences significant impacts due to global change <sup>8,9</sup>. Measurable  
59 negative effects on wildlife have already occurred, such as population decreases of numerous seabird  
60 species <sup>10,11</sup>, including the complete loss of emperor penguin (*Aptenodytes forsteri*) colonies <sup>12,13</sup>. The  
61 vanishing of these colonies has been attributed to strong El Niño events, rise in local mean annual air  
62 temperature, strong winds, and/or decline in seasonal sea ice duration. Climate change is also  
63 expected to result in human access to new ice-free fishing areas <sup>14</sup>, whereby seabirds and marine  
64 mammals will have to compete for food with industrial fisheries and may even become by-catch <sup>15</sup>.  
65 The accumulation of anthropogenic pressures on these fragile ecosystems urgently requires effective  
66 protection <sup>16</sup>.

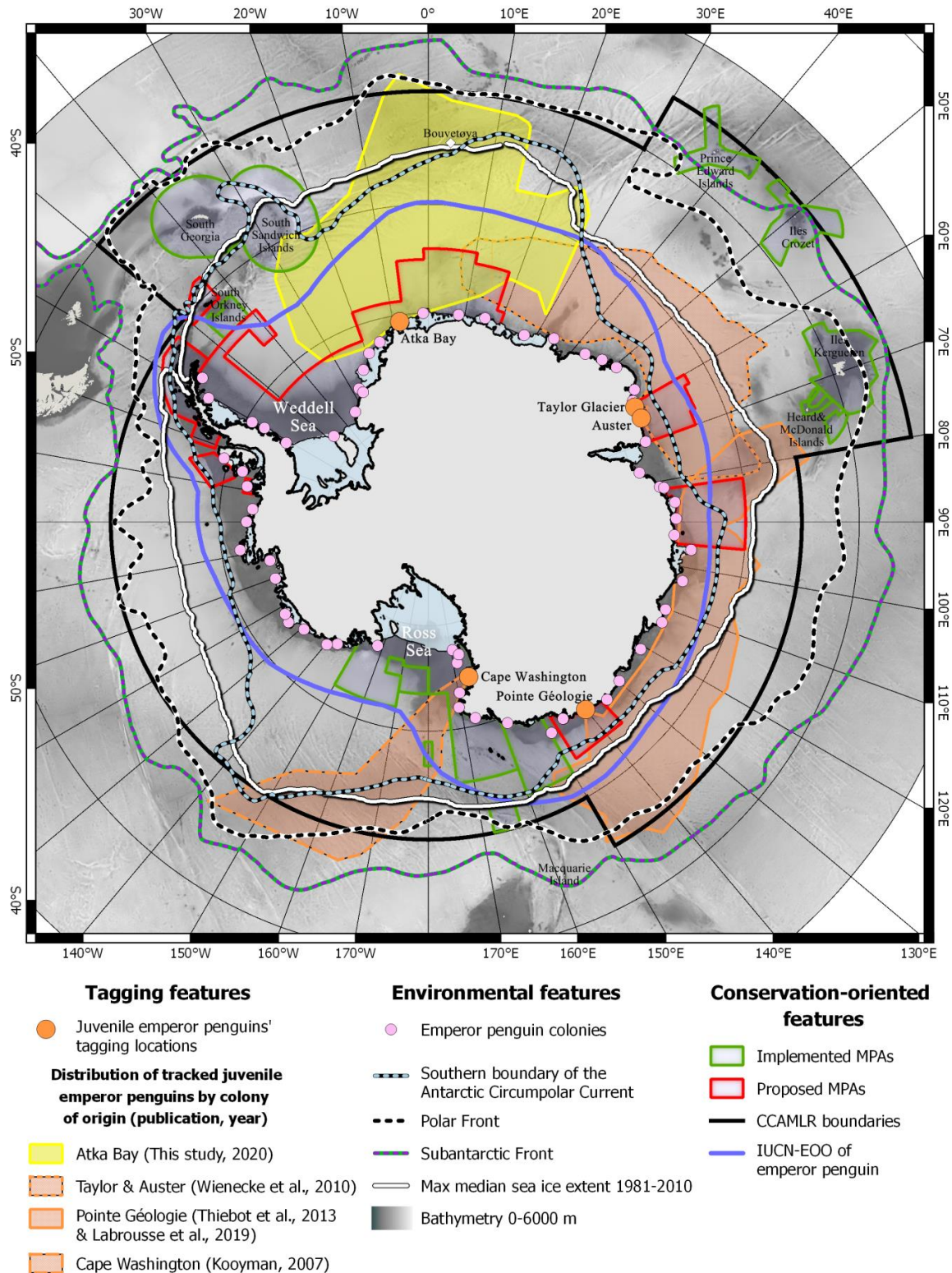
67 The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is the  
68 governing body in charge of conservation issues in the Southern Ocean. CCAMLR's mandate includes  
69 the implementation of conservation measures, such as the establishment of Marine Protected Areas  
70 (MPAs) and the regulation of the fishing industry, through quota allocations and gear limitations<sup>17</sup>.  
71 Within the CCAMLR, conservation measures are based on the best scientific data available, including  
72 the distribution and demography of marine predators<sup>18,19</sup>. Similarly, the International Union for  
73 Conservation of Nature (IUCN)'s Red List of Threatened Species depicts the extent of occurrence  
74 (EEO) of each species, i.e. all the known, inferred or projected sites of present occurrence of the  
75 species' adults excluding cases of vagrancy<sup>20</sup>. Such knowledge serves then as a reference for policy  
76 making on the implementation of conservation measures. Consequently, providing novel data, in  
77 areas that have never been surveyed or on data-deficient population classes like juveniles enhances  
78 the conservation governance perspective for a species and its habitat.

79 Currently, 12% of the waters inside the CCAMLR boundaries are protected, with only 4.6% as no-take  
80 areas. This includes the Ross Sea and waters around South Orkney Islands<sup>16</sup>. Since 2002, the CCAMLR  
81 has been working on establishing a network of MPAs around Antarctica, but the implementation of  
82 three new MPAs in East Antarctica, the Weddell Sea, and at the Antarctic Peninsula has been  
83 difficult. But even when implemented, the new MPAs would protect only 22% of the Southern Ocean  
84 inside the CCAMLR boundaries<sup>16</sup>, which is significantly less than the IUCN recommended protection  
85 target of 30% of each marine habitat<sup>21</sup>. Furthermore, assessments and recommendations are based  
86 on limited and incomplete data. For instance, in the Weddell Sea, home to one-third of the global  
87 emperor penguin population, no tracking studies have been conducted so far; thus, very little is  
88 known about the penguins' at-sea distribution in this area.

89 The Emperor penguin is considered an iconic and ecologically important species of Antarctica. Its  
90 colony sites and at-sea movements have been the basis of previous discussions of conservation  
91 priorities, either in terms of MPAs<sup>4</sup>, Important Bird Areas<sup>22,23</sup> or Areas of Ecological Significance

92 (AESs<sup>24</sup>). With a population currently estimated at *ca.* 270 000 breeding pairs in 61 known colonies  
93 around the continent<sup>25</sup>, the species is severely threatened by global warming and expanding fishing  
94 activities in the Southern Ocean<sup>15,26</sup>, facing the risk to be nearly extinct within this century<sup>27</sup>. The  
95 most effective actions to protect the Emperor penguin from anthropogenic impacts would be a  
96 reduction in greenhouse gas emissions<sup>26,27</sup> as well as the establishment of MPAs throughout its  
97 habitat range<sup>26</sup>. However, little is known about the early life at sea of emperor penguins, even  
98 though their survival is crucial for the viability of the global population<sup>28</sup>. To date, a total of only 48  
99 juvenile emperor penguins have been tracked. Moreover, tracking has been done only in the Ross  
100 Sea and East Antarctica (Table 1), even though for the designation of MPAs, it is fundamental to  
101 know their distribution at the circum-Antarctic scale<sup>4,6,7</sup>.

102 The aim of this study was to bridge this gap in knowledge by equipping 6-months-old emperor  
103 penguin chicks with ARGOS satellite platforms that transmit the birds' locations several times each  
104 day. Birds were tagged before their initial departure from their colony of origin at Atka Bay (70°37'S,  
105 08°09'W) near the south eastern limit of the Weddell Sea (Fig. 1). We recorded their journey during  
106 their first year at sea (Fig. 1 and Supplementary Table 1). To assess the habitat range used by the  
107 juvenile emperor penguins at the scale of the Southern Ocean, we incorporated the distribution of all  
108 previously tracked juvenile emperor penguins into our analysis (Fig. 1; <sup>29–32</sup>). We find that juveniles  
109 travel beyond the boundaries of existing and planned conservation and management areas,  
110 demonstrating that conservation efforts in the Southern Ocean are insufficient to protect emperor  
111 penguins.



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**Fig. 1. Overlap between existing and planned conservation zones and the distribution of juvenile emperor penguins tracked to date in the Southern Ocean.** Distribution areas of juveniles are indicated by colored polygons. MPAs: Marine Protected Areas; CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources; IUCN-EOO: International Union for Conservation of Nature Extent Of Occurrence (i.e. the extent of occurrence of the species considered by the IUCN <sup>33</sup>).

## 118 Results

119 The tracking data from our study show that juvenile emperor penguins travelled north of 50°S (the  
120 lowest recorded latitude was 48.37°S), which is 600 km further north than previously recorded (Table  
121 1). Two of the eight tagged birds reached the South Sandwich Islands region in winter (late June until  
122 at least July) before their ARGOS platforms stopped transmitting. Thus, with three of the eight birds  
123 reaching sub-Antarctic areas, the presence of juvenile emperor penguins in these waters should be  
124 considered common rather than unusual behavior. All tagged juveniles reached the southern  
125 boundary of the Antarctic Circumpolar Current (ACC), and five of the tagged birds remained between  
126 the southern ACC boundary and the Antarctic Polar Front for prolonged time periods (> 46 days). One  
127 bird travelled north of the Polar Front <sup>29,32</sup>. The penguin tracks over a full year (polygon  
128 encompassing the area covered by the tracks, Supplementary Fig. 1) covered an area of 5.1 million  
129 km<sup>2</sup> (Fig. 1 and Fig. 2, Table 1), nearly 1.4 times larger than the largest previously reported  
130 distribution of juvenile emperor penguins from their colony of origin (Table 1).

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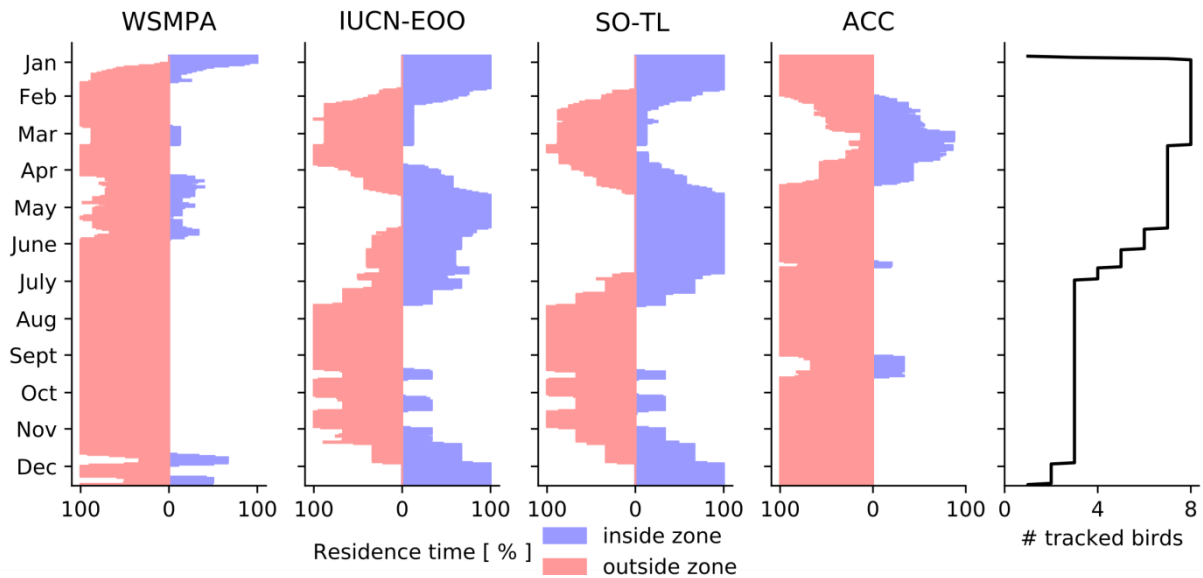
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137 **Table 1. Tracking studies of juvenile emperor penguins at sea.**

Colony	Colony coordinates	Colony population estimate*	Number of birds tracked	Mean tracking duration (days)	Maximal distance from colony (km)	Northernmost latitude reached	Distribution area (millions km <sup>2</sup> )	%** in ACC area	%** in SO - TL	%** in IUCN - EOO	%** in CCAMLR area	%** in MPAs	Publication
Cape Washington	74.58 S, 165.48 E	11808	10	64	2845	56.9°S	1.7	54.6	73.5	14.6	73.5	4.4	Kooyman et al. 2007 <sup>29</sup>
Pointe Géologie	66.66°S, 140.00°E	2456	21	171	3503	53.76°S	3.6	75.9	62.7	35.8	98.0	13.5	Labrousse et al. 2019 <sup>32</sup> ; Thiebot et al. 2013 <sup>31</sup>
Auster Taylor Glacier	67.38°S, 64.03°E 67.47°S, 60.88°E	7855 519	10 7	121 113	2343 1570	56.25°S 54.23°S	3.3 1.7	60.7 87.3	79.1 67.7	61.4 43.4	100 100	6.7 9.3	Wienecke et al. 2010 <sup>30</sup>
Atka Bay	70.62°S, 08.15°W	9657	8	221	2474	48.37°S	5.1	19.3	60.7	51.4	99.2	16.3	This study
Mean	/	6459	11.2	138	2547	/	3.1	59.6	68.7	41.3	94.1	10.0	/
sd	/	4798	5.6	59.9	707.9	/	1.4	25.9	7.6	17.7	11.6	4.9	/

138 Colony details (location and size), tracking survey metrics (duration, distance, distribution) and proportion of the  
 139 distribution area of tracked juveniles for each colony falling within the main oceanographic features (ACC, SO-TL) and  
 140 conservation related areas (IUCN, CCAMLR, MPAs) of the Southern Ocean. \* Number of breeding pairs<sup>25</sup>. \*\* Proportion of  
 141 the distribution area falling within the mentioned feature. ACC: Antarctic Circumpolar Current; SO-TL: Southern Ocean  
 142 Treaty Limits (i.e. at the parallel of 60°S as defined in the Antarctic Treaty); CCAMLR: Commission for the Conservation of  
 143 Antarctic Marine Living Resources; IUCN-EOO: International Union for Conservation of Nature Extent Of Occurrence (i.e. the  
 144 extent of occurrence of the species considered by the IUCN<sup>33</sup>; MPAs: Marine Protected Areas.





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**Fig. 2. Proportion of time that the eight tagged juvenile emperor penguins from the Atka Bay colony spent either inside or outside the main conservation related areas (WSMPA, IUCN-EOO) and oceanographic features (SO-TL, ACC) of the Atlantic sector of the Southern Ocean.** Daily average across all individuals computed over hourly data points. WSMPA: Weddell Sea Marine Protected Area; IUCN-EOO: International Union for Conservation of Nature Extent Of Occurrence (i.e. the extent of occurrence of the species considered by the IUCN <sup>33</sup>; SO-TL: Southern Ocean Treaty Limits (i.e. at the parallel of 60°S as defined in the Antarctic Treaty); ACC: Antarctic Circumpolar Current.

Juvenile emperor penguins from the Weddell Sea area had a seasonal travel pattern similar to that of those tracked in other sectors of the Southern Ocean. After leaving their colony, juveniles migrated northward towards and into the ACC where they remained for  $37 \pm 24$  days. Juvenile emperor penguins commonly ranged outside the limits of the Southern Ocean (i.e. the parallel of 60°S as defined by the Antarctic Treaty, hereafter referred to as SO-Treaty); some birds travelled outside the CCAMLR boundaries (Fig. 1, Supplementary Table 1). Over the course of April, juveniles migrated southward towards the pack ice to spend the winter (Supplementary Fig. 2). In this study, the juvenile penguins spent only  $51.1 \pm 13.3\%$  of their time inside the IUCN-EOO of the species, which is based on the estimated adult distribution (Supplementary Fig. 2). Moreover, the time spent inside the area varied significantly across months ( $p < 1e-05$ ; Fig. 2). In August (winter), all penguins were outside and travelled up to 1260 km north of the IUCN-EOO, whereas they were mostly inside in January and May. When considering the data from all studies,  $41.3 \pm 17.7\%$  of the observed

164 distribution areas of juvenile emperor penguins fell within the IUCN-EOO (Table 1). Juveniles from  
165 the Cape Washington colony in the Ross Sea travelled up to 1500 km outside the IUCN-EOO.

166 Taken together, the EOO of emperor penguin defined by the IUCN is underestimating the current  
167 habitat range of the species. Existing and planned MPAs cover on average only  $10.0 \pm 4.9\%$  of the  
168 estimated distribution areas (Table 1). Regarding the time spent inside protected areas, juvenile  
169 emperor penguins from the Atka Bay colony, which is located inside the proposed Weddell Sea  
170 Marine Protected Areas (WSMPA, the largest currently proposed MPA in the Southern Ocean), left  
171 the MPA's boundaries after  $9 \pm 4$  days in January, and remained only  $10.6 \pm 7.5\%$  of their time inside  
172 the boundaries (Fig. 2). Only during summer (January and December) did the juveniles spend a  
173 considerable amount of time inside the WSMPA ( $47.9 \pm 23.8\%$  and  $31.1 \pm 13.4\%$ , respectively). All  
174 tagged penguins were outside the WSMPA's boundaries in February and from July to November (Fig.  
175 2).

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## 177 Discussion

178 Penguins are considered umbrella species of the Southern Ocean's ecosystem<sup>34</sup>. Monitoring their  
179 population trend and distribution is therefore essential for biodiversity conservation. The common  
180 approach for designating boundaries of MPAs focuses on protecting the breeding segment of  
181 populations<sup>35</sup>. We argue that this might not be sufficient for species for which juvenile and adult  
182 ranges do not overlap, and we point out that the habitat range of juvenile penguins requires also a  
183 high level of protection. Indeed, juveniles are more vulnerable than adults as their foraging skills  
184 (including their ability to dive, to capture prey, and to find productive feeding grounds) are not yet  
185 fully developed, and their experience to escape predators is minimal<sup>36</sup>. Moreover, juvenile survival  
186 can have a critical impact on the population dynamics, especially in long-lived species<sup>37</sup>. Emperor  
187 penguins start breeding earliest at age 4-5 years, lay only one egg per pair and year, and only have an

188 annual chance of 55% to bring a chick to fledging<sup>27</sup>. This low fecundity, projected to decrease under  
189 future warming scenarios<sup>27</sup>, makes the survival of immature individuals, which represent about one  
190 quarter of the total population<sup>28</sup>, particularly critical for the recruitment into breeding populations  
191 and thus the species' viability<sup>38</sup>. Moreover, in contrast to adults, the dispersal behavior of juveniles is  
192 one of the main processes by which long-lived species will be able to adapt to the ongoing rapid  
193 environmental change. A vast travel range allows them to explore possible alternative feeding and  
194 breeding grounds<sup>39</sup>. Therefore, for successful conservation we need to consider the habitat range of  
195 all age classes.

196 Our findings reveal that juveniles commonly spent a considerable amount of time outside the  
197 species' IUCN-EOO and outside the limits of existing or planned MPAs in the Southern Ocean (Fig. 1,  
198 Table 1 and Supplementary Table 1). Consequently, if protection measures were based solely on the  
199 current IUCN-EOO of the species, as it stands, given its focus on adult occurrences due to the  
200 insufficient data for juveniles, this could lead to inefficient decisions for the future protection of the  
201 species. Furthermore, all studies including ours have reported that juveniles visit the highly  
202 productive ACC area during their first journey at sea, where the Antarctic Polar Front appears to act  
203 as an ecological barrier. During the most vulnerable stage of their life, the penguins' dispersive  
204 behavior leads them outside the SO-Treaty and CCAMLR limits into waters where they are likely to  
205 encounter and compete with fisheries (see<sup>23,40</sup> for data on fisheries activity). In accordance with the  
206 CCAMLR's ecosystem-based fisheries management approach, the presence of this critical fragment of  
207 the emperor penguin population should be considered by the CCAMLR when allocating fishing  
208 quotas and zones; especially in the current context where several CCAMLR fishing states are lobbying  
209 for an increase of the spatial and temporal distribution of catches and fisheries<sup>41</sup>.

210 A growing body of evidence indicates the ongoing threats to penguins. Trathan and colleagues<sup>26</sup>  
211 recently advocated for a reclassification of the Emperor penguin on the IUCN Red List from the  
212 current "Near Threatened" status to "Vulnerable" or "Endangered", together with the classification

213 as an “Antarctic Specially Protected Species” by the Antarctic Treaty. Our data support this call for  
214 better protection by also pointing out the need to include all age-classes and age-specific threats into  
215 the classification assessment <sup>4,7</sup>. Furthermore, in the context of the vast range of emperor penguins  
216 and other marine top predators <sup>4</sup>, our data argue in favor of a circumpolar integrated systems of  
217 marine protected areas in the Southern Ocean that consider large parts of the offshore Antarctic  
218 Convergence area. This could be achieved, for instance by combining migratory corridors with static  
219 and dynamic MPAs (i.e. MPAs that rapidly evolve in space and time in response to changes in the  
220 ocean and its users; <sup>42</sup>), to create an ecological connected network <sup>43</sup> that would provide more  
221 effective protection to the Southern Ocean ecosystem <sup>16</sup>.

## 222 **Materials and Methods**

### 223 **Study site and instrumentation**

224 Our study was conducted at the Atka Bay emperor penguin colony (70°37’S, 08°09’W) near (~ 10 km)  
225 the German Antarctic research base “Neumayer Station III”. In January 2019, we equipped eight 6-  
226 month-old chick emperor penguins with satellite communicating SPOT-367 ARGOS platforms  
227 (Wildlife Computers, Redmond, WA 98052, USA). The ARGOS platforms were programmed to  
228 transmit their identification every day at 4, 6, 10, 16, 19 and 21:00 GMT, corresponding to time  
229 points with optimum ARGOS satellite coverage over the Weddell Sea (ARGOS CLS, Toulouse, France).

230 To minimize drag, the ARGOS platforms were deployed on the lower back of the birds <sup>44,45</sup>. The  
231 streamlined devices were attached to the feather with adhesive tape (Tesa tape 4651, Beiersdorf AG,  
232 Hamburg, Germany) and secured with three cable ties (Panduit PLTM1.5M-C0 142\*2.6 mm, Panduit  
233 Corp, Illinois, USA). We then applied epoxy glue (Loctite EA 3430, Loctite, Henkel AG., Düsseldorf,  
234 Germany) on the mounting to increase waterproofing and robustness <sup>46,47</sup>.

### 235 **Estimation of the at-sea distribution of juvenile emperor penguins from the Atka Bay colony**

#### 236 *Location filtering*

237 ARGOS locations are associated with spatial error ellipses. These spatial errors can range from a few  
238 hundred meters to several kilometers<sup>48,49</sup>. Erroneous locations were filtered out using a speed filter  
239 from the R package ‘*argos filter*’<sup>50</sup> with the maximum travel speed fixed at 15 km/h following similar  
240 studies on emperor penguins<sup>32,51</sup>.

#### 241 *Interpolation of locations at a regular time step*

242 We used a state-space modelling approach<sup>52</sup> to estimate hourly locations. Specifically, a Kalman  
243 filter, which accounted for location error, was applied using the R package ‘*crawl*’<sup>53</sup>, and Continuous-  
244 time Correlated Random Walk (CRW) models were used to predict locations at a regular time step  
245 interval of 1 h<sup>52,54</sup>.

#### 246 **Estimation of the colony-specific distribution area for juvenile emperor penguins**

247 In addition to the 8 birds tracked in our study, 48 juvenile emperor penguins from 4 different  
248 colonies were previously tracked<sup>29–32</sup>, see Table 1 for the details on the colonies). Data of these  
249 previously acquired bird journeys are available as maps in the respective publications. We  
250 georeferenced these tracking maps using the QGIS software. We subsequently plotted the main  
251 corner points encompassing the tracks of all birds from each colony (Supplementary Fig. 1). We  
252 obtained the distribution of juvenile emperor penguins by computing the concave hull envelope for  
253 each dataset using the ‘*ConcaveHull*’ plugin<sup>55</sup>. Envelopes from the same colony<sup>31,32</sup> were merged to  
254 consider only one polygon per colony (referred to as distribution area), including one for the Atka  
255 Bay colony. The size of each distribution area was calculated with the ‘*raster*’ package in R<sup>56</sup> and is  
256 reported in Table 1. Due to the significant overlap of Auster and Taylor Glacier juvenile distribution<sup>30</sup>  
257 and the proximity (132 km) of the two sites<sup>57</sup>, for visualization purposes, the tracks of the birds from  
258 Auster and Taylor Glacier colonies are shown in the same polygon in Fig. 1. However, the distribution  
259 areas were computed separately for each colony.

#### 260 **Ecological features**

261 The locations of the Southern Ocean fronts and the Antarctic Circumpolar Current boundaries (ACC,  
262 <sup>58</sup>) were downloaded from <https://gis.ccamlr.org> <sup>59</sup>.

263 The bathymetry at one-minute horizontal spatial resolution was obtained from the ETOPO1 Global  
264 Relief Model provided by the NOAA National Geophysical Data Center <sup>60</sup>.

265 Sea ice concentrations (ranging from 0-100%) were obtained from Advanced Microwave Scanning  
266 Radiometer (AMSR-2) satellite estimates of daily sea ice concentration at 3.125 km resolution from  
267 the University of Bremen (<https://seaice.uni-bremen.de/data/amr2/>) <sup>61</sup>. The sea ice edge contour  
268 was defined by the 15% sea ice concentration <sup>62,63</sup> (Supplementary Fig. 2).

269 The maximum and minimum median sea ice extent from 1981-2010 presented in Supplementary Fig.  
270 1 and Supplementary Fig. 2 were obtained from the National Snow and Ice Data Center NSDIC <sup>64</sup>  
271 implemented in the '*Quantarctica3*' package <sup>65</sup> of the QGIS software.

## 272 **Conservation oriented features**

273 The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) planning  
274 domains and existing Antarctic Marine Protected Areas (MPAs) were obtained from  
275 <https://gis.ccamlr.org> <sup>59</sup>. The proposed Weddell Sea Marine Protected Area boundaries (WSMPA, <sup>66</sup>)  
276 and the proposed East Antarctic Marine Protected Area boundaries (EAMPA, <sup>67</sup>) were obtained from  
277 [www.mpatlas.org](http://www.mpatlas.org) <sup>68</sup>. The Domain 1 MPA proposal <sup>69</sup> was drawn from [www.mpatlas.org](http://www.mpatlas.org) <sup>68</sup>. The South  
278 Georgia and South Sandwich Islands Marine Protected Area (SGSSIMPA) and the sub-Antarctic MPAs  
279 boundaries were downloaded from [www.protectedplanet.net](http://www.protectedplanet.net).

280 The International Union for Conservation of Nature (IUCN) extent of occurrence (EOO) of the  
281 Emperor penguin species was obtained from [www.iucnredlist.org](http://www.iucnredlist.org) <sup>70</sup>.

## 282 **Assessing the overlap between bird distribution and conservation oriented areas**

283 The average residency time that each of the birds equipped in our study spent inside existing or  
284 proposed conservation oriented areas of the Southern Ocean was computed on a daily, weekly or  
285 monthly basis, or averaged over the total tracking period.

286 We tested whether the observed monthly-averaged residency time changed significantly over the  
287 course of a year using the Kruskal-Wallis rank sum tests. For all tests, the significance threshold was  
288 set at  $p=0.05$ . Statistical analyses were performed using the software R v. 3.5.0<sup>71</sup> and QGIS v. 2.18.18  
289<sup>72</sup> with the data package ‘*Quantarctica3*’<sup>65</sup>.

## 290 Data and materials availability

291 All data generated or analysed during this study will be available in the Movebank data repository at  
292 <https://www.movebank.org/>.

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## 469 **Competing interests**

470 Authors declare no competing interests.

471

472 **Author contributions**

473 AH and CLB conceived the ideas and designed the methodology and protocols. AH, OE and CLB,  
474 conducted fieldwork. AH and KH analysed data. AH, DZ, OE and CLB interpreted the results. AH, DZ,  
475 BF and CLB led the writing of manuscript. All authors edited and proofread the paper.