# **Oceanic seabirds chase tropical cyclones** 1

- 2
- Francesco Ventura<sup>1,9,10,\*</sup>; Neele Sander<sup>2,3</sup>; Paulo Catry<sup>4</sup>; Ewan Wakefield<sup>5</sup>; Federico De 3
- Pascalis<sup>6</sup>; Philip L. Richardson<sup>2</sup>; José Pedro Granadeiro<sup>7</sup>; Mónica C. Silva<sup>8</sup>; Caroline C. 4
- Ummenhofer<sup>2</sup>. 5
- 6
- 1. Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA 7
- 2. Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods 8
- Hole, MA, USA 9
- 3. Christian-Albrechts-Universität zu Kiel, Geomar Helmholtz-Center for Ocean Research, Kiel, Germany 10 11
- 4. MARE Marine and Environmental Sciences Centre / ARNET Aquatic Research 12
- Network, Ispa Instituto Universitário, Lisbon, Portugal 13
- 5. Department of Geography, Durham University, Durham, UK 14
- 6. Area Avifauna Migratrice, Istituto Superiore per la Protezione e la Ricerca Ambientale 15
- (ISPRA), Ozzano dell'Emilia, Italy 16
- 7. Centre for Environmental and Marine Studies (CESAM), Departmento de Biologia 17
- Animal, Universidade de Lisboa, Lisbon, Portugal 18
- 8. Centre for Ecology, Evolution and Environmental Changes (cE3c), Departmento de 19
- Biologia Animal, Universidade de Lisboa, Lisbon, Portugal 20
- 21
- 9. X/Twitter: @FraVentoora 22
- 10. Lead contact 23
- \*Correspondence: fraventura.92@gmail.com 24

#### **Summary** 25

In late summer and autumn, the passage of intense tropical cyclones can profoundly perturb oceanic and coastal ecosystems. Direct negative effects on individuals and marine communities can be dramatic, especially in the coastal zone  $1-4$ , but cyclones can also enhance pelagic primary and secondary production 5–9. However, cyclone impacts on open ocean marine life remain poorly understood. Here, we investigate their effects on the foraging movements of a wide-ranging higher-predator, the Desertas petrel (*Pterodroma deserta*), in the mid-latitude North Atlantic during hurricane season. Contrary to previously studied pelagic seabirds in tropical and mid-latitude regions  $10,11$ , Desertas petrels did not avoid cyclones by altering course, nor did they seek calmer conditions within the cyclone eye. Approximately one-third of petrels tracked from their breeding colony interacted with approaching cyclones. Upon encountering strong winds, the birds reduced ground speed, likely by spending less time in flight. A quarter of birds followed cyclone wakes for days and over thousands of kilometres, a behaviour documented here for the first time. Within these wakes, tail wind support was higher than along alternative routes. Furthermore, at the mesoscale (hours − weeks and 100s of km), surface chlorophyll sharply increased and sea surface temperature dropped, suggesting direct effects on ocean stratification, primary production and therefore presumably prey abundance and accessibility for surface-feeding petrels. We therefore hypothesise that cyclone wakes provide both predictably favourable wind conditions and foraging opportunities. As such, cyclones may have positive net effects on the demography of many mid-latitude pelagic seabirds and, likely, other marine top-predators. 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46

47

#### **Keywords** 48

cyclone; extreme weather; foraging ecology; *Pterodroma*; seabird; storm; wind. 49

50

#### **Results** 51

From June to November in the Northern Hemisphere, tropical cyclones commonly form in the tropics and can move into the mid-latitude regions, self-advecting and driven northeastward in the North Atlantic by the prevailing westerlies, before dissipating. Cyclones have catastrophic impacts on coastal and terrestrial ecosystems, affecting everything from individuals to species distributions and community diversity  $1-4$ . Strong winds can negatively impact seabirds by forcing them inland or to other unfavourable habitats <sup>12,13</sup>, reducing foraging opportunities or effectiveness  $14$ , directly injuring them and causing secondary effects on dependent offspring <sup>15,16</sup>. Indeed, in coastal and island settings, seabird movements have been observed and interpreted as avoiding intense cyclonic winds  $17$ . Avoidance behaviours range from remaining ashore  $10,18$ , circumnavigating the cyclone edge  $^{10}$  or flying towards the system eye  $^{11}$ . 52 53 54 55 56 57 58 59 60 61 62

63

Despite these insights, the impacts of tropical cyclones on seabirds and other pelagic species remain poorly understood. In the open ocean, the behavioural responses of pelagic seabirds to cyclones should not be exclusively assessed in terms of the risk of being injured 64 65 66

or displaced inland. For instance, strong winds could facilitate rapid, goal-oriented travel for foraging seabirds  $19$ . Furthermore, by enhancing turbulent mixing, strong winds can trigger sudden changes in the physical and biological environment and boost primary and secondary production over short (days to weeks) and more prolonged (weeks to months) time scales  $5-9$ . 67 68 69 70 71

72

Here, we test whether cyclones have either negative or positive impacts on pelagic seabirds by determining whether their movement is consistent with avoidance of or attraction to these systems. As model organism we use Desertas petrels (*Pterodroma deserta*), a pelagic seabird belonging to the order Procellariiformes (comprising albatrosses, petrels and shearwaters), breeding in the Madeiran archipelago during the North Atlantic hurricane season. As suggested by their order name (from the Latin word '*Procella*', storm), procellariiform seabirds are frequently sighted in regions of heavy seas, are associated with tempests in our collective imagination  $20$ , and were regarded by ancient seafarers as bad omens, being forerunners of an imminent storm <sup>21</sup>. We analysed 43 GPStracked central-place-foraging trips made by 33 petrels, recorded during incubation over four breeding seasons, plus the tracks of all tropical cyclones occurring during the same study years, obtained from the International Best Track Archive for Climate Stewardship (IBTrACS) database  $^{22}$  (Figure 1). The tracks of petrels and cyclones were interpolated to 1 h and their time-stamps synchronised. We focussed on two stages of the petrels' movement responses to cyclones: an initial approach from long distances (up to 900 km), followed by the movements at closer range when the petrels were near the cyclone eye or along the wake. 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89

90

To investigate the long-distance movement responses of petrels to cyclones we used an integrated step selection analysis (iSSA)<sup>23</sup>. We carried out two analyses. In the first iSSA, we asked whether birds avoid (or move towards) cyclones. We found that birds did not avoid cyclones. Instead, they approached them, showing a selection for steps towards the eye (Figure S5). Upon reaching areas within 400 km of the eye, birds did no longer move towards it. This could be an artefact due to the smaller sample size, or highlight a behavioural response: getting closer than 400 km from the eye of a cyclone could be detrimental, which is also suggested by the observed reduction of ground speed (and possible increase in landing behaviour) under strong winds (see below). In the second iSSA, we asked: given an interaction, are these interactions solely due to birds selecting specific wind angles (i.e., is it simply the preference for specific wind angles that drives petrels towards cyclones), or do birds direct their movements towards cyclones even after accounting for the effect of the wind? As expected for birds that optimise their foraging movements by making efficient use of the windscape  $24$ , petrels selected tailwinds and crosswind and avoided headwinds. Moreover, after accounting for the wind angle, birds showed a tendency to select steps closer to the eye (see Figure S5), suggesting that the petrels' movement towards cyclones is an active process and not simply the outcome of the birds' preferences for specific wind conditions. 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106 107 108

109

After the initial long-range approach, the tracks of nearly one-third of the tagged petrels (i.e., 10 petrels, 10 trips) met an active cyclone, reaching areas within 200 km of its eye. In such conditions, petrels experienced a median wind speed equal to 49 km/h (interquartile-interval IQI =  $40 - 56$  km/h; maximum wind speed =  $86$  km/h) and median wave height (significant height of combined wind waves and swell) of 4.4 m (IQI = 4.0 – 5.6 m; maximum wave height =  $8.4$  m). In locations further than 200 km away from the eye, the birds experienced lower wind speeds (median =  $24 \text{ km/h}$ , IQI =  $18 - 31 \text{ km/h}$ ) and wave heights (median = 1.9 m, IQI =  $1.5 - 2.4$  m). These differences were statistically significant (Welch Two Sample t-test;  $t = 15.16$ ,  $d.f. = 90.54$ , p-value < 0.001 for wind speed;  $t = 21.50$ , d.f. = 90.46, p-value < 0.001 for wave height). Importantly, the aforementioned wind speeds are most likely underestimates of the real conditions experienced by the petrels in proximity of cyclones <sup>25</sup>. Using generalised additive mixed effects models, we found that Desertas petrels reduced their ground speed under strong winds ( $\geq 70<sup>th</sup>$  percentile of wind speeds experienced by all birds, i.e.  $\geq$  29.65 km/h) (Figure S1 and Figure S2). This behaviour was evident when petrels sharply reduced their movement speed under the strong winds of an approaching cyclone (Figure 1). 110 111 112 113 114 115 116 117 118 119 120 121 122 123 124 125

126

We then considered instances during which petrels followed the wake of cyclones, i.e. those consecutive movement segments in which petrels were behind the cyclone eye's position (i.e., to the west of an eastbound cyclone) and reached < 200 km from the path realised by the cyclone as it passes through the water. Approximately half of the tagged individuals (i.e., 15 petrels, 17 trips) did this at some point. During these events, petrels used waters perturbed by the passage of 6 major cyclones, following cyclone wakes for a median distance of 1077 km (IQI = 566 – 2235 km) and a median duration of 47 hours (IQI = 16 – 94 hours). Notably, 10 petrels followed a cyclone for at least 1.5 days, flying along a cyclone wake for a median of 2112 km (IQI =  $1143 - 2434$  km) and 92 hours (IQI =  $48 - 122$ hours) (Figure 2 and Video S1). Throughout these long movement bouts, petrels flew with positive wind support, calculated as the wind speed component in the direction of flight (or tail wind component "TWC"). The TWC experienced was significantly higher than that achievable had the birds undertaken alternative plausible trajectories (by 3 km/h, paired ttest,  $t = 2.98$ , d.f. = 9, p = 0.02), which we simulated by rotating the observed movements by 30° to the Northeast or Southeast (Figure S3). 127 128 129 130 131 132 133 134 135 136 137 138 139 140 141

142

Prevailing winds shape both the petrels' long clockwise movements  $24$  and the cyclone trajectories, leading to relatively conserved geometries of bird and cyclone tracks. Therefore, we assessed whether petrels remained close to cyclones for longer that expected by chance alone. To do so, we considered all petrel tracks and estimated the duration of observed interactions between petrels and cyclones (defined as the number of petrel track points within 200 km of the eye or the wake of a cyclone). The observed interactions were compared to the (simulated) interactions that petrels would have performed with cyclones occurring in different years. On average, observed interactions lasted 26 h per trip, whereas the simulated interactions were 13 h long. This difference was significant (Mann-143 144 145 146 147 148 149 150 151

Whitney test,  $W = 20218$ , p-value = 0.003), indicating that petrels used areas perturbed by cyclones more frequently than expected by chance. 152 153

154

Finally, due to the small spatial variability of the typical paths of cyclones across the North Atlantic, we investigated whether petrels followed the wakes of active cyclones concurrent to their foraging movements, or the birds associated with wakes of cyclones occurring earlier in the season. By computing the Fréchet distance between petrel movements and cyclones  $26$ , we found that the petrel tracks were significantly closer and more similar in shape to the trajectories of recent cyclones (Mann-Whitney test,  $W = 21$ , p-value < 0.0001), suggesting that the association between petrels and wakes is underpinned by mechanisms acting over short time scales. 155 156 157 158 159 160 161 162

163

Indeed, as soon as a day or a few days after the passage of all 6 cyclones in the study, upwelling, wind-induced vertical mixing and turbulence led to a sharp increase in surface chlorophyll and a decrease in sea surface temperatures along their wakes (Figure 3 and Figure S4). Compared to other sections of their tracks, petrels foraging along cyclone wakes flew over waters significantly more enriched in chlorophyll (paired t-test, t = 2.51,  $d.f. = 16$ ,  $p = 0.02$ ), but the wind conditions experienced (in terms of TWC and wind angle relative to the bird direction of movement) were not significantly different from those during the rest of the tracks (TWC: paired t-test,  $t = 0.82$ , d.f. = 16,  $p = 0.43$ ; relative wind angle: paired t-test,  $t = 0.19$ , d.f. = 16,  $p = 0.85$ ). 164 165 166 167 168 169 170 171 172

173

### **Discussion** 174

By using dynamic soaring  $27,28$  to extract energy from the wind, Desertas petrels make some of the longest foraging movements of any animal during breeding  $24$ , seemingly anticipating and responding to the available wind conditions at an ocean-wide scale. With a foraging distribution encompassing a vast oceanic region in the North Atlantic during the hurricane season, Desertas petrels likely encounter cyclonic systems repeatedly throughout the course of their long lives. It seems exceedingly unlikely that petrels found themselves along the path of cyclones by chance or because of poor movement decisions. Rather, the petrels are likely to have evolved specific behaviours to minimise risks and exploit the potential positive effects of foraging in a system regularly perturbed by cyclones  $29$ . It has been suggested that seabirds use indirect cues to anticipate wind conditions, possibly in combination with simple rules of thumb learnt empirically, similar to those followed by seafarers before the advent of modern weather forecasting  $30,31$ . Seabirds may sense meteorological cues that could be used to forecast the approach of cyclones, such as the typical changes in air temperature, wind direction, barometric pressure, cloud cover and precipitation, wave heights and direction of propagation of storm swell  $32-34$ . Thus equipped, birds can implement manoeuvres to avoid cyclones  $10,11$ or, as showed in this work, to follow them for days and over thousands of kilometres. 175 176 177 178 179 180 181 182 183 184 185 186 187 188 189 190 191

192

Desertas petrels exclusively forage over deep waters  $^{24}$  and encounter cyclones thousands of km away from the coastline, placing the birds at no immediate risk of being blown 193 194

inland. Avoiding storms by adding circumnavigating trajectories to the already long trips may not be possible if such detours would entail a delayed return to the colony or flying over poor foraging areas <sup>14</sup>. Yet, cyclones seem to provide foraging advantages, rather than presenting unavoidable, unfavourable occurrences for these oceanic birds. The first iSSA indicated that petrels do not avoid cyclones but, rather, move towards the eye of the incoming cyclone until reaching a distance of approximately 400 km from it. At that point, as the storm draws nearer, petrels fly neither towards nor away from the system's centre. Under the intense winds of an approaching storm, birds seem to reduce their ground speed. While the temporal resolution of our GPS dataset is too low to directly assess landing behaviour, it is possible that the petrels experience hurricane-force winds and waves of up to 8m sitting on the water. The reduced ground speeds under strong tailwinds may reflect sections in which the birds were drifting on the surface of the water, pushed by the strong winds. This could be due to limiting flight in potentially dangerous conditions that could cause mechanical damage to outstretched wings, but it could also result from foraging or undertaking upwind prey searching manoeuvres. Ultimately, it is difficult to determine whether birds actively seek cyclones hundreds of kilometres away, or whether the movement towards the eye is underpinned by the wind, which shapes the trajectories of petrels and cyclones and may force them, at some point, to converge. Regardless, our results conclusively show that petrels do not exhibit avoidance movements with respect to an incoming storm, nor do they seek calmer conditions within the cyclone eye (diameter of 20-50 km), as the birds stop moving towards the eye at a distance of approximately 400 km. The second iSSA retained both wind angle and distance from cyclone eye as significant explanatory variables affecting petrels' movement, suggesting that the attraction towards cyclones is not simply driven by the effect of the wind. After the passage of a cyclone, as its eye moves away, the selection of movement steps towards the eye results in an overall movement following the wake of the outbound cyclone. Indeed, 15 out of 33 tracked birds used waters perturbed by the passage of cyclones to a higher extent than expected by chance. In this context, the energetically efficient dynamic soaring flight may play a critical role. In fact, less efficient flyers, more constrained in their foraging movements, may not be able to exploit the opportunities opened up by the passage of cyclones and be more vulnerable to the associated risks  $14$ . The hypermobile Desertas petrels, instead, carried out long movement sections following the cyclone wakes for thousands of km and several days, with some of their trips closely resembling the path of the storm (Figure 2 and Video S1). We suggest that the usage of such areas yields flight and foraging advantages, as discussed below. 195 196 197 198 199 200 201 202 203 204 205 206 207 208 209 210 211 212 213 214 215 216 217 218 219 220 221 222 223 224 225 226 227 228 229

230

Petrels flying along the wakes of cyclones experienced significantly higher wind support (i.e., tail wind component) compared to plausible alternative (simulated) paths, suggesting that the eastbound passage of cyclones may bring predictably favourable conditions for petrels flying eastward. However, the wind conditions experienced along wakes were not significantly different from the winds experienced throughout other sections of the petrel trips. This is somewhat unsurprising, as petrels optimise their movements in relation to 231 232 233 234 235 236

wind during their entire tracks  $^{24}$ , including when following cyclone wakes. However, wind optimisation may not be the only factor at play. 237 238

239

Cyclones modify the structure of the mixed surface layer and of the entire water column over which they pass, causing upwelling and vertical mixing of warmer surface water with deeper, cooler and nutrient-rich waters, inducing large-scale changes in both the physical and biological environment  $5-9$ . Immediately after the passage of cyclonic systems in our study area, upwelling and turbulence induced by strong winds brought phytoplankton towards the surface, resulting in a sharp drop in sea surface temperature and a net increase of surface chlorophyll. Enhanced mixing could also bring zooplankton and other weakly swimming prey closer to the surface, either through direct advection or by erosion of the thermocline affecting the distribution of organisms undertaking diel vertical migration, making them more evenly distributed across the mixed layer. In turn, taxis (i.e. consumers moving towards higher concentrations of their prey) could affect the vertical faunal distribution across the water column  $\frac{8}{7}$ , leading to greater near-surface densities of mesopelagic fish and cephalopods upon which petrels prey. At the mesoscale (100s of km and hours − weeks), seabirds and other marine predators take advantage of dynamic features that enhance and modulate vertical mixing, planktonic aggregations, and mesopelagic communities such as fronts and eddies  $35-37$ . Our findings suggest that, by affecting ocean mixing and, in turn, the depth and accessibility of prey, cyclones too may represent a critical – yet overlooked – feature that can be exploited by foraging pelagic seabirds and, potentially, other top-predators inhabiting mid-latitude oceanic ecosystems. 240 241 242 243 244 245 246 247 248 249 250 251 252 253 254 255 256 257 258

# 259

### **ACKNOWLEDGEMENTS** 260

We thank Joanie Van de Walle, Théo Michelot, Andrew Solow, Alessandro Bocconcelli, James Price, Simon Thorrold, Etienne Rouby, Bilgecan Şen and Christian Che-Castaldo for useful discussions. Fieldwork was made possible by Dília Menezes and Instituto das Florestas e da Conservação da Natureza – Madeira. F.V. is supported by the Postdoctoral Scholar Program at Woods Hole Oceanographic Institution, with fundings from the John E. Sawyer Fund and the John H. Steele Endowment. Data collection was supported by the Fundação para a Ciência e a Tecnologia (FCT) through projects: (1) PTDC/BIA-EVL/28565/2017; (2) UIDB/00329/2020 and UIDB/BIA/00329/2020, https://doi.org/10.54499/UIDB/00329/2020 (cE3c); (3) UIDB/04292/2020, UIDP/04292/2020 (MARE) and LA/P/0069/2020 (ARNET); and (4) UIDP/50017/2020, UIDB/50017/2020 and LA/P/0094/2020 (CESAM). 261 262 263 264 265 266 267 268 269 270 271

272

## **AUTHOR CONTRIBUTIONS** 273

C.C.H., F.V. and N.S. conceived the study. F.V., N.S., P.C., E.W. and F.D.P. designed the analyses, with input from P.L.R., J.P.G. and M.C.S. P.C., J.P.G. and M.C.S. contributed data. F.V. and F.D.P. processed the data and carried out the analyses. F.V. and C.C.H. wrote the first draft of the manuscript and all authors provided feedback and edited the manuscript drafts. 274 275 276 277 278

# 279

#### **Declaration of interests** 280

The authors declare no competing interests. 281

282

**Figure 1. The foraging movements of Desertas petrels during hurricane season**. (A) Foraging trips made by Desertas petrels (*Pterodroma deserta*) during incubation in 2015, 2016, 2017 and 2019 (grey, 33 individuals, 43 trips) from Bugio Island (yellow dot). During 17 foraging trips (black), 15 petrels used areas within 200 km of 6 tropical cyclones (cyclone tracks red; sections of petrel trips < 200 km from a cyclone blue). (B) Examples of two petrel tracks which intersected the track of a cyclone (hurricane Gaston). Rows correspond to individual birds and columns subsequent times. The underlying colours depict contemporary wind speed (darker colours = stronger winds) and direction. The white and black paths are the trajectories of cyclone and petrels, respectively. The triangles and dots are concurrent hourly hurricane and petrel locations, respectively, with simultaneous bird and cyclone locations depicted using the same colour. The shaded area is the area of maximum wind speeds extracted from IBTrACS  $^{22}$ . As the hurricane draws near, the petrels reduce their ground speed likely by sitting on the water. 283 284 285 286 287 288 289 290 291 292 293 294 295

296

**Figure 2. Petrels' movements along the wake of cyclones.** (A) Map showing the path of hurricane Gaston (in red) and the concurrent foraging movements (in black) of a petrel from the breeding colony of Bugio (yellow dot). The underlying colours depict the sea surface temperature anomaly (blue = cold anomalies).The sea surface temperatures are anomalously low in the cyclone's wake. (B) Tracks of 9 petrels that followed cyclone wakes over the greatest distance. The yellow dot is the breeding colony of Bugio; the cyclones are shown as a solid red line, with the shaded red area depicting the associated area of maximum wind speeds. The black tracks depict the petrel movements, and the blue segments are those within a maximum of 200 km from the storm's wake (see also Video S1). 297 298 299 300 301 302 303 304 305 306

**Figure 3. Surface chlorophyll-A evolution for locations traversed by cyclones.** Chlorophyll-a was measured from seven days before up to a month after the passage of the cyclone (marked by the blue vertical dotted line at timestep  $= 0$ ). The y-axes of different panels are on different scales. In addition, the chlorophyll-A profile was calculated for grid points within radii of 200 and 400 km of locations traversed by the cyclones. Rug plots show days on which tracked petrels used areas within 200 km of the wake of each cyclone. See also the sea surface temperature anomaly evolution for locations traversed by cyclones in Figure S4. 308 309 310 311 312 313 314 315

316

307

- **STAR Methods** 317
- 318
- **RESOURCE AVAILABILITY** 319
- 320
- **Lead contact** 321
- Further information and requests for resources and reagents will be addressed by the lead 322
- contact Francesco Ventura (fraventura.92@gmail.com). 323
- 324

#### **Materials availability** 325

- This research did not generate new unique reagents. 326
- 327

#### **Data and code availability** 328

The raw tracking dataset is stored on the Seabird Tracking Database (https://www.seabirdtracking.org). The raw cyclone tracks are available at the International Best Track Archive for Climate Stewardship (IBTrACS) database (https://www.ncei.noaa.gov/products/international-best-track-archive). Annotated tracking data, as well as R scripts to fully replicate the analysis, are available at the Figshare repository https://figshare.com/authors/Francesco\_Ventura/7066628. 329 330 331 332 333 334

335

#### **EXPERIMENTAL MODEL AND SUBJECT DETAILS** 336

The analysis were carried out on tracking datasets collected on Desertas petrels (*Pterodroma deserta*) during the incubation phase of the breeding seasons of 2015, 2016, 2017 and 2019. 337 338 339

340

#### **METHOD DETAILS** 341

342

#### **Bio-logging data and cyclone tracks** 343

Desertas petrels are endemic to Bugio Island, (32°25′35″N 16°29′10″W) in the Madeiran archipelago. Their small population size is estimated at ca. 200 nesting pairs. Breeding petrels were tracked during incubation of the breeding seasons of 2015, 2016, 2017 and 2019 (see Table S1) using GPS loggers (nanoFix, Pathtrack Ltd, wt of 3.4g). The loggers were either 3.0 g or 7.4 g, representing (with added tape) less than 3% of the average adult body mass (300 g  $^{38}$ ). Tracks were collected at either 2h (n=21 trips) or 1h (n=22 trips) resolution from 33 individuals. Cyclone tracks were obtained from the International Best Track Archive for Climate Stewardship (IBTrACS) database, which stores the most comprehensive record of all major tropical cyclones and the coordinates of the cyclones' eye at a temporal resolution of  $3 h^{22}$ . 344 345 346 347 348 349 350 351 352 353

354

### **Data processing** 355

Cyclone and petrel tracks were interpolated to 1 h resolution to synchronise the time stamps of each foraging track to the respective concurrent cyclones. Interpolation was carried out using the great circle method from the move package  $39$  in R. The following environmental variables were downloaded and associated to each location along the petrels' and cyclones' tracks, based on the coordinates and the time stamp: wave height (m); zonal (u) and meridional (v) wind vectors (m/s); sea surface temperature anomaly (SSTA,  $^{\circ}$ C); chlorophyll A (mg/m<sup>3</sup>). The chlorophyll A and SSTA evolution in response to cyclones was quantified by extracting the chlorophyll A and SSTA values measured at all points along each cyclone track, from seven days before and up to a month after the 356 357 358 359 360 361 362 363 364

passage of each cyclone. Wave height and zonal and meridional wind vectors at 10m altitude were downloaded from ERA5 global reanalysis models (Copernicus Climate Change Service,  $40$ , at a spatial and temporal resolution of 0.25 $^{\circ}$  and 1 hour. The vectors were used to calculate horizontal wind speed and direction. Tail wind component (TWC, i.e., the wind speed component in the direction of the bird movement) and relative wind angle (i.e., the wind direction relative to bird movement direction) were calculated for each point along the tracks following Ventura et al., 2020<sup>24</sup>. Multi-scale Ultra-high Resolution sea surface temperature anomaly <sup>41</sup> was dowloaded from NOAA (https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41), at a spatial resolution of 0.01° and at a daily temporal resolution. Surface observation data of chlorophyll-A mass concentration in sea water was downloaded from the E.U. Copernicus Marine Service Information Global Ocean Colour at a daily temporal resolution and at a spatial resolution of  $4$ (https://data.marine.copernicus.eu/product/OCEANCOLOUR\_GLO\_BGC\_L4\_MY\_009\_10 365 366 367 368 369 370 371 372 373 374 375 376 377 378

4/download?dataset=cmems\_obs-oc\_glo\_bgc-plankton\_my\_l4-gapfree-multi-4km\_P1D).

- 379
- 
- 380

#### **Step selection analysis** 381

We carried out two integrated step selection analyses (iSSA)  $^{23}$ . This framework allows the estimation of the strength of selection or avoidance of particular environmental variables conditional on movement constraints<sup>23</sup>. The first iSSA was formulated to test whether petrels exhibit avoidance responses with respect to cyclones. For this analysis, we retained all movement steps during which birds were within a distance from the eye of 900 km. We also tested whether different avoidance/selection responses happen at different spatial scales by building a set of 7 additional models. Each model was fit to a data subset retaining all steps within a given distance from the eye, from 800 km to 200 km (i.e. one subset retained all steps within 800 km, one subset comprised all steps within 700 km, and so on and so forth until 200 km). The second iSSA was designed to test whether the observed interactions between petrels and cyclones are exclusively driven by the wind, or whether birds move towards cyclones and follow their wake even after accounting for the wind. For this analysis, we considered the 17 tracks in which petrels interacted with active cyclones (i.e., reached areas within 200 km of the eye or the wake), excluding the segment where birds were returning to the colony, identified as in  $42$ . In both analyses, for each observed step along a foraging track, we created 50 at-sea random steps using step lengths and turning angles sampled from the theoretical distribution fitted to the observed steps (Gamma for step length and Von Mises for angle). We ensured that all the random steps created were at sea via a thinning procedure. We then computed, for each step (observed or random) the distance to the eye (km) of the closest ongoing cyclone and the wind direction relative to the direction of movement ("Δangle", which was tested as explanatory variable in the second iSSA). To account for individual differences in selection, we fitted conditional Poisson models with individual specific random slopes for the covariate and stratum-(sets of one observed and 50 matched random steps) specific intercept  $43$ . Distance from the eye was inserted as negative independent variable (e.g.,  $0 =$  eye, -10: 10 km away from the eye), as well as the natural logarithm of step length and the cosine of turning 382 383 384 385 386 387 388 389 390 391 392 393 394 395 396 397 398 399 400 401 402 403 404 405 406 407

angle (to account for movement processes  $^{23}$ ) and  $\Delta$ angle (in the second iSSA). Variables were scaled and centred to aid model convergence. We evaluated selection or avoidance using population β-coefficients from the Poisson model and 95% confidence intervals (see Figure S5). 408 409 410 411

412

#### **QUANTIFICATION AND STATISTICAL ANALYSIS** 413

414

#### **Are interactions with cyclones more frequent than expected by chance?** 415

We used a randomisation procedure to test whether the observed extent of interaction between petrels and cyclones was higher than expected by chance. We considered all the 43 foraging trips collected in our study. For each trip, we calculated the number of track points (i.e. the number of hours) in which the petrel was within 200 km of the eye or the wake of a cyclone. This represented the observed (real) extent of interaction between petrels and cyclones. Then, we calculated the number of points falling within 200 km of the eye or the wake of a cyclone that occurred during the same day and month of each foraging trip, but in different years (from 2000 to 2019, i.e. the last study year). The latter represented the simulated extent of interaction with cyclones. On average, the real interactions lasted 26.30 h per trip, whereas the simulated interactions were 12.78 h long. The extent of real interactions was significantly greater than the extent of simulated interactions (Mann-Whitney test,  $W = 20218$ , p-value = 0.003). 416 417 418 419 420 421 422 423 424 425 426 427

428

#### **Are foraging trips more similar to concurrent or to previous cyclones?** 429

Due to the stereotyped geometry of cyclone paths, petrels following the wake of an ongoing cyclone may instead be following a wake from earlier in the season. We therefore investigated whether the tracks of petrels interacting with cyclones more closely matched the most recent cyclone better than the tracks of previous cyclones. To do so, for each trip we computed the Fréchet distance <sup>44</sup> between the petrel trajectory and: (i) the observed cyclones concurrent to the foraging movement; (ii) the cyclones that occurred earlier in the season, before the onset of the foraging trip. We used the Fréchet distance for our comparative analysis, a shape-based metric that can be applied to trajectories with different lengths, particularly suited to detect similarity of movement trajectories  $^{26}$ . With this metric, larger values indicate lower similarity. On average, the Fréchet distance between petrel tracks and concurrent cyclones was equal to 24.10, whereas the distance between tracks and previous cyclones was equal to 60.35. Petrel tracks were significantly more similar to concurrent cyclones than to those occurring earlier in the season (Mann-Whitney test,  $W = 21$ , p-value < 0.0001). 430 431 432 433 434 435 436 437 438 439 440 441 442 443

444

#### **Ground speed under strong winds** 445

To quantitatively investigate whether petrels altered their ground speed in response to strong winds, we first identified the locations along the tracks in which petrels experienced wind intensities equal to or greater than the 70% percentile (i.e., wind intensities  $\geq$  29.65 km/h). We then used generalised additive mixed effects models (GAMM) from the R package mgcv<sup> $45$ </sup> to investigate the effect of wind on the birds' ground 446 447 448 449 450

speed (see Figure S1 and Figure S2). GAMMs were used to capture potential nonmonotonic relationships between ground speed and wind. The response variable ground speed (km/h) was modelled using the gamma distribution. The explanatory variables considered were: wind intensity (km/h) and wind direction relative to bird movement direction (in degrees), both included as cubic regression splines with shrinkage. The tensor product interaction between the two variables was also tested as a candidate covariate in the model. Individual level random effects were used to account for the dependency between observations collected on the same bird. The GAMM showed that the ground speed was non-linearly affected by Δangle, wind intensity and their interaction. In particular, petrels attained lowest ground speeds under strong (> 60 km/h) tail to quartering tail winds (Δangle between 0° to 60°) and with headwinds (Figure S1 and Figure S2). 451 452 453 454 455 456 457 458 459 460 461 462

463

#### **Tail wind support along cyclone wakes** 464

We identified the tracks of nine petrels flying along the wake of cyclones for at least 2 days. A simulation framework was used to investigate whether, along these sections, petrels experienced higher wind support (in terms of tail wind component, "TWC") compared to equivalent movement sections rotated by 30° Northeastward and Southeastward (see Figure S3). To do so, for each petrel, we calculated the first and last point of the movement bout along a storm wake, i.e. the first and last point in which a petrel was within 200 km of the wake. We then calculated the (real) TWC experienced by the bird. TWC was calculated as: 465 466 467 468 469 470 471 472

*TWC = wind speed \* cosine (bird bearing – wind direction)*, 473

where wind direction is expressed in the same reference system as the bearing of the animal (i.e.,  $0^{\circ}$  = Northward, or southerly;  $90^{\circ}$  = Eastward, or westerly;  $180^{\circ}$  = Southward, or northerly; 270° = Westward, or easterly). Then, starting from the same initial point and maintaining the same timestamp and same trip configuration as the real data, we rotated each movement segment along the storm wake by 30° Northward and Southward, one degree at a time, generating 60 simulated rotated tracks. We extracted the wind conditions along these rotated segments and calculated the associated TWC. Throughout the real movement bouts along the storm wake, petrels flew with positive wind support (on average equal to 5.9 km/h,  $sd = 4$  km/h). The latter was significantly higher (by a difference of 2.8 km/h) than the hypothetical mean TWC experienced along the rotated movement sections (paired t-test,  $t = 3.05$ , d.f. = 8,  $p = 0.016$ ). 474 475 476 477 478 479 480 481 482 483 484

485

#### **Chlorophyll A and wind conditions within and outside cyclone wakes** 486

We considered the 17 tracks in which petrels reached waters within 200 km of the eye or the wake of a cyclone. For those tracks, we compared the chlorophyll A and wind conditions (in terms of TWC and relative wind angle) experienced by the birds when they used waters along cyclones or not. The chlorophyll A experienced was significantly higher (paired t-test,  $t = 2.51$ , d.f. = 16,  $p = 0.02$ ) when birds used waters perturbed by cyclonic activity (by  $0.056$  mg/m<sup>3</sup>, on average) than elsewhere along their tracks. Wind conditions experienced were, however, not significantly different, both considering TWC (paired t-487 488 489 490 491 492 493

- test,  $t = 0.82$ , d.f. = 16,  $p = 0.43$ ) and wind angle relative to bird movement (paired t-test,  $t =$ 494
- 0.19, d.f. = 16,  $p = 0.85$ ). 495
- 496
- **Video S1. Desertas petrel foraging movement following the wake of a cyclone, related** 497
- **to Figure 2.** A central-place foraging trip made by one Desertas petrels (*Pterodroma deserta*), 498
- in black, associating extensively with the wake of a cyclone (in white). The underlaying 499
- grid depicts contemporary wind speed (darker colours = stronger winds) and direction. The shaded light area is the area of maximum wind speeds extracted from IBTrACS. 500 501
- Sections of the tracks < 200 km from a cyclone are depicted in red. 502







- twilight zone. Proc. Natl. Acad. Sci. U. S. A. *116*, 17187–17192. 605
- https://doi.org/10.1073/pnas.1903067116. 606
- 37. Arostegui, M.C., Gaube, P., Woodworth-Jefcoats, P.A., Kobayashi, D.R., and Braun, C.D. (2022). Anticyclonic eddies aggregate pelagic predators in a subtropical gyre. Nature *609*. https://doi.org/10.1038/s41586-022-05162-6. 607 608 609
- 38. Warham, J. (1996). The behaviour, population biology and physiology of the petrels (Academic Press). 610 611
- 39. Kranstauber, B., Smolla, M., and Scharf, A.K. (2018). move: visualizing and analyzing animal track data. R package version 3.1. 0. 612 613
- 40. Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., et al. (2020). The ERA5 global reanalysis. Q. J. R. Meteorol. Soc. *146*, 1999–2049. https://doi.org/https://doi.org/10.1002/qj.3803. 614 615 616
- 41. Chin, T.M., Vazquez-Cuervo, J., and Armstrong, E.M. (2017). A multi-scale high-resolution analysis of global sea surface temperature. Remote Sens. Environ. *200*, 154–169. https://doi.org/https://doi.org/10.1016/j.rse.2017.07.029. 617 618 619
- 42. Wakefield, E.D., Phillips, R.A., Matthiopoulos, J., Fukuda, A., Higuchi, H., Marshall, G.J., and Trathan, P.N. (2009). Wind field and sex constrain the flight speeds of central-place foraging albatrosses. Ecol. Monogr. *79*, 663–679. 620 621 622
- 43. Muff, S., Signer, J., and Fieberg, J. (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. J. Anim. Ecol. *89*, 80–92. https://doi.org/10.1111/1365-2656.13087. 623 624 625
- 44. Alt, H., and Godau, M. (1995). Computing the Fréchet distance between two polygonal curves. Int. J. Comput. Geom. \& Appl. *5*, 75–91. 626 627
- 45. Wood, S.N. (2006). Generalized Additive Models: An Introduction with R (Chapman and Hall/CRC). 628 629



**Citation on deposit:** Ventura, F., Sander, N., Catry, P., Wakefield, E., De Pascalis, F., Richardson, P. L., Granadeiro, J. P., Silva, M. C., & Ummenhofer, C. C. (2024). Oceanic seabirds chase tropical cyclones. Current Biology, 34(14), 3279-3285.

# <https://doi.org/10.1016/j.cub.2024.06.022>

**For final citation and metadata, visit Durham Research Online URL:** <https://durham-research.worktribe.com/record.jx?recordid=2614794> **Copyright statement:** This accepted manuscript is licensed under the Creative Commons Attribution 4.0 licence.

<https://creativecommons.org/licenses/by/4.0/>