1 Oceanic seabirds chase tropical cyclones

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25 Summary

26 In late summer and autumn, the passage of intense tropical cyclones can profoundly 27 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 28 enhance pelagic primary and secondary production ⁵⁻⁹. However, cyclone impacts on open 29 ocean marine life remain poorly understood. Here, we investigate their effects on the 30 foraging movements of a wide-ranging higher-predator, the Desertas petrel (Pterodroma 31 32 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 33 petrels did not avoid cyclones by altering course, nor did they seek calmer conditions 34 35 within the cyclone eye. Approximately one-third of petrels tracked from their breeding colony interacted with approaching cyclones. Upon encountering strong winds, the birds 36 37 reduced ground speed, likely by spending less time in flight. A quarter of birds followed 38 cyclone wakes for days and over thousands of kilometres, a behaviour documented here 39 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 40 sharply increased and sea surface temperature dropped, suggesting direct effects on ocean 41 stratification, primary production and therefore presumably prey abundance and 42 accessibility for surface-feeding petrels. We therefore hypothesise that cyclone wakes 43 provide both predictably favourable wind conditions and foraging opportunities. As such, 44 45 cyclones may have positive net effects on the demography of many mid-latitude pelagic 46 seabirds and, likely, other marine top-predators.

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48 Keywords

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

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Results 51

52 From June to November in the Northern Hemisphere, tropical cyclones commonly form in 53 the tropics and can move into the mid-latitude regions, self-advecting and driven north-54 eastward in the North Atlantic by the prevailing westerlies, before dissipating. Cyclones 55 have catastrophic impacts on coastal and terrestrial ecosystems, affecting everything from individuals to species distributions and community diversity 1-4. Strong winds can 56 negatively impact seabirds by forcing them inland or to other unfavourable habitats ^{12,13}, 57 reducing foraging opportunities or effectiveness ¹⁴, directly injuring them and causing 58 secondary effects on dependent offspring ^{15,16}. Indeed, in coastal and island settings, 59 60 seabird movements have been observed and interpreted as avoiding intense cyclonic winds ¹⁷. Avoidance behaviours range from remaining ashore ^{10,18}, circumnavigating the 61 cyclone edge¹⁰ or flying towards the system eye¹¹. 62

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Despite these insights, the impacts of tropical cyclones on seabirds and other pelagic 64 species remain poorly understood. In the open ocean, the behavioural responses of pelagic 65

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.

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73 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 74 75 attraction to these systems. As model organism we use Desertas petrels (Pterodroma 76 deserta), a pelagic seabird belonging to the order Procellariiformes (comprising albatrosses, 77 petrels and shearwaters), breeding in the Madeiran archipelago during the North Atlantic 78 hurricane season. As suggested by their order name (from the Latin word 'Procella', 79 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 80 seafarers as bad omens, being forerunners of an imminent storm ²¹. We analysed 43 GPS-81 82 tracked central-place-foraging trips made by 33 petrels, recorded during incubation over 83 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 84 85 (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' 86 87 movement responses to cyclones: an initial approach from long distances (up to 900 km), 88 followed by the movements at closer range when the petrels were near the cyclone eye or 89 along the wake.

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

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

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127 We then considered instances during which petrels followed the wake of cyclones, i.e. 128 those consecutive movement segments in which petrels were behind the cyclone eye's 129 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 130 individuals (i.e., 15 petrels, 17 trips) did this at some point. During these events, petrels 131 used waters perturbed by the passage of 6 major cyclones, following cyclone wakes for a 132 133 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 134 cyclone wake for a median of 2112 km (IQI = 1143 – 2434 km) and 92 hours (IQI = 48 – 122 135 136 hours) (Figure 2 and Video S1). Throughout these long movement bouts, petrels flew with 137 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 138 139 achievable had the birds undertaken alternative plausible trajectories (by 3 km/h, paired t-140 test, t = 2.98, d.f. = 9, p = 0.02), which we simulated by rotating the observed movements by 141 30° to the Northeast or Southeast (Figure S3).

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Prevailing winds shape both the petrels' long clockwise movements ²⁴ and the cyclone 143 trajectories, leading to relatively conserved geometries of bird and cyclone tracks. 144 145 Therefore, we assessed whether petrels remained close to cyclones for longer that expected 146 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 147 148 points within 200 km of the eye or the wake of a cyclone). The observed interactions were 149 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, 150 whereas the simulated interactions were 13 h long. This difference was significant (Mann-151

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

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155 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 156 157 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 158 cyclones ²⁶, we found that the petrel tracks were significantly closer and more similar in 159 shape to the trajectories of recent cyclones (Mann-Whitney test, W = 21, p-value < 0.0001), 160 161 suggesting that the association between petrels and wakes is underpinned by mechanisms 162 acting over short time scales.

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Indeed, as soon as a day or a few days after the passage of all 6 cyclones in the study, 164 upwelling, wind-induced vertical mixing and turbulence led to a sharp increase in surface 165 166 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 167 wakes flew over waters significantly more enriched in chlorophyll (paired t-test, t = 2.51, 168 d.f. = 16, p = 0.02), but the wind conditions experienced (in terms of TWC and wind angle 169 170 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 171 172 angle: paired t-test, t = 0.19, d.f. = 16, p = 0.85).

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174 Discussion

By using dynamic soaring ^{27,28} to extract energy from the wind, Desertas petrels make some 175 of the longest foraging movements of any animal during breeding ²⁴, seemingly 176 anticipating and responding to the available wind conditions at an ocean-wide scale. With 177 178 a foraging distribution encompassing a vast oceanic region in the North Atlantic during the hurricane season, Desertas petrels likely encounter cyclonic systems repeatedly 179 180 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. 181 Rather, the petrels are likely to have evolved specific behaviours to minimise risks and 182 183 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 184 conditions, possibly in combination with simple rules of thumb learnt empirically, similar 185 to those followed by seafarers before the advent of modern weather forecasting ^{30,31}. 186 Seabirds may sense meteorological cues that could be used to forecast the approach of 187 188 cyclones, such as the typical changes in air temperature, wind direction, barometric pressure, cloud cover and precipitation, wave heights and direction of propagation of 189 190 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. 191

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

inland. Avoiding storms by adding circumnavigating trajectories to the already long trips 195 may not be possible if such detours would entail a delayed return to the colony or flying 196 over poor foraging areas ¹⁴. Yet, cyclones seem to provide foraging advantages, rather than 197 198 presenting unavoidable, unfavourable occurrences for these oceanic birds. The first iSSA 199 indicated that petrels do not avoid cyclones but, rather, move towards the eye of the 200 incoming cyclone until reaching a distance of approximately 400 km from it. At that point, 201 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 202 203 speed. While the temporal resolution of our GPS dataset is too low to directly assess 204 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 205 206 may reflect sections in which the birds were drifting on the surface of the water, pushed by 207 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 208 foraging or undertaking upwind prey searching manoeuvres. Ultimately, it is difficult to 209 determine whether birds actively seek cyclones hundreds of kilometres away, or whether 210 211 the movement towards the eye is underpinned by the wind, which shapes the trajectories 212 of petrels and cyclones and may force them, at some point, to converge. Regardless, our 213 results conclusively show that petrels do not exhibit avoidance movements with respect to 214 an incoming storm, nor do they seek calmer conditions within the cyclone eye (diameter of 215 20-50 km), as the birds stop moving towards the eye at a distance of approximately 400 216 km. The second iSSA retained both wind angle and distance from cyclone eye as 217 significant explanatory variables affecting petrels' movement, suggesting that the attraction towards cyclones is not simply driven by the effect of the wind. After the 218 219 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, 220 221 15 out of 33 tracked birds used waters perturbed by the passage of cyclones to a higher 222 extent than expected by chance. In this context, the energetically efficient dynamic soaring 223 flight may play a critical role. In fact, less efficient flyers, more constrained in their 224 foraging movements, may not be able to exploit the opportunities opened up by the 225 passage of cyclones and be more vulnerable to the associated risks ¹⁴. The hypermobile 226 Desertas petrels, instead, carried out long movement sections following the cyclone wakes 227 for thousands of km and several days, with some of their trips closely resembling the path 228 of the storm (Figure 2 and Video S1). We suggest that the usage of such areas yields flight 229 and foraging advantages, as discussed below.

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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 wind during their entire tracks ²⁴, including when following cyclone wakes. However,
wind optimisation may not be the only factor at play.

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Cyclones modify the structure of the mixed surface layer and of the entire water column 240 over which they pass, causing upwelling and vertical mixing of warmer surface water with 241 242 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 243 study area, upwelling and turbulence induced by strong winds brought phytoplankton 244 245 towards the surface, resulting in a sharp drop in sea surface temperature and a net 246 increase of surface chlorophyll. Enhanced mixing could also bring zooplankton and other 247 weakly swimming prey closer to the surface, either through direct advection or by erosion 248 of the thermocline affecting the distribution of organisms undertaking diel vertical 249 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 250 faunal distribution across the water column⁸, leading to greater near-surface densities of 251 mesopelagic fish and cephalopods upon which petrels prey. At the mesoscale (100s of km 252 253 and hours - weeks), seabirds and other marine predators take advantage of dynamic 254 features that enhance and modulate vertical mixing, planktonic aggregations, and mesopelagic communities such as fronts and eddies ³⁵⁻³⁷. Our findings suggest that, by 255 affecting ocean mixing and, in turn, the depth and accessibility of prey, cyclones too may 256 represent a critical – yet overlooked – feature that can be exploited by foraging pelagic 257 258 seabirds and, potentially, other top-predators inhabiting mid-latitude oceanic ecosystems. 259

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273 AUTHOR CONTRIBUTIONS

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.

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280 Declaration of interests

- 281 The authors declare no competing interests.
- 282

283 Figure 1. The foraging movements of Desertas petrels during hurricane season. (A) Foraging trips made by Desertas petrels (Pterodroma deserta) during incubation in 2015, 284 2016, 2017 and 2019 (grey, 33 individuals, 43 trips) from Bugio Island (yellow dot). During 285 286 17 foraging trips (black), 15 petrels used areas within 200 km of 6 tropical cyclones 287 (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 288 correspond to individual birds and columns subsequent times. The underlying colours 289 290 depict contemporary wind speed (darker colours = stronger winds) and direction. The 291 white and black paths are the trajectories of cyclone and petrels, respectively. The triangles 292 and dots are concurrent hourly hurricane and petrel locations, respectively, with 293 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 294 295 near, the petrels reduce their ground speed likely by sitting on the water.

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297 Figure 2. Petrels' movements along the wake of cyclones. (A) Map showing the path of 298 hurricane Gaston (in red) and the concurrent foraging movements (in black) of a petrel 299 from the breeding colony of Bugio (yellow dot). The underlying colours depict the sea 300 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 301 302 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 303 304 maximum wind speeds. The black tracks depict the petrel movements, and the blue 305 segments are those within a maximum of 200 km from the storm's wake (see also Video 306 S1). 307

Figure 3. Surface chlorophyll-A evolution for locations traversed by cyclones. 308 309 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 310 panels are on different scales. In addition, the chlorophyll-A profile was calculated for grid 311 312 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. 313 See also the sea surface temperature anomaly evolution for locations traversed by cyclones 314 315 in Figure S4.

- 316
- 317 STAR Methods
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- 319 **RESOURCE AVAILABILITY**
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- 321 Lead contact

- 322 Further information and requests for resources and reagents will be addressed by the lead
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325 Materials availability

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

328 Data and code availability

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

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336 EXPERIMENTAL MODEL AND SUBJECT DETAILS

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.

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341 METHOD DETAILS

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

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

354

355 Data processing

356 Cyclone and petrel tracks were interpolated to 1 h resolution to synchronise the time 357 stamps of each foraging track to the respective concurrent cyclones. Interpolation was 358 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 359 petrels' and cyclones' tracks, based on the coordinates and the time stamp: wave height 360 361 (m); zonal (u) and meridional (v) wind vectors (m/s); sea surface temperature anomaly 362 (SSTA, °C); chlorophyll A (mg/m³). The chlorophyll A and SSTA evolution in response to 363 cyclones was quantified by extracting the chlorophyll A and SSTA values measured at all 364 points along each cyclone track, from seven days before and up to a month after the

passage of each cyclone. Wave height and zonal and meridional wind vectors at 10m 365 366 altitude were downloaded from ERA5 global reanalysis models (Copernicus Climate Change Service, ⁴⁰), at a spatial and temporal resolution of 0.25° and 1 hour. The vectors 367 368 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 369 370 angle (i.e., the wind direction relative to bird movement direction) were calculated for each point along the tracks following Ventura et al., 2020²⁴. Multi-scale Ultra-high 371 Resolution sea surface temperature anomaly ⁴¹ was dowloaded from NOAA 372 (https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41), at a spatial resolution 373 374 of 0.01° and at a daily temporal resolution. Surface observation data of chlorophyll-A mass 375 concentration in sea water was downloaded from the E.U. Copernicus Marine Service 376 Information Global Ocean Colour at a daily temporal resolution and at a spatial resolution 377 of 4 km (https://data.marine.copernicus.eu/product/OCEANCOLOUR_GLO_BGC_L4_MY_009_10

4/download?dataset=cmems_obs-oc_glo_bgc-plankton_my_l4-gapfree-multi-4km_P1D).

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381 **Step selection analysis**

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

angle (to account for movement processes ²³) and Δ 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).

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413 QUANTIFICATION AND STATISTICAL ANALYSIS

414

414 415 Are interactions with cyclones more frequent than expected by chance?

416 We used a randomisation procedure to test whether the observed extent of interaction 417 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 418 419 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 420 petrels and cyclones. Then, we calculated the number of points falling within 200 km of 421 the eye or the wake of a cyclone that occurred during the same day and month of each 422 423 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 424 425 interactions lasted 26.30 h per trip, whereas the simulated interactions were 12.78 h long. 426 The extent of real interactions was significantly greater than the extent of simulated 427 interactions (Mann-Whitney test, W = 20218, p-value = 0.003).

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

430 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 431 432 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 433 we computed the Fréchet distance ⁴⁴ between the petrel trajectory and: (i) the observed 434 435 cyclones concurrent to the foraging movement; (ii) the cyclones that occurred earlier in the 436 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 437 438 different lengths, particularly suited to detect similarity of movement trajectories ²⁶. With 439 this metric, larger values indicate lower similarity. On average, the Fréchet distance 440 between petrel tracks and concurrent cyclones was equal to 24.10, whereas the distance 441 between tracks and previous cyclones was equal to 60.35. Petrel tracks were significantly 442 more similar to concurrent cyclones than to those occurring earlier in the season (Mann-443 Whitney test, W = 21, p-value < 0.0001).

444

445 Ground speed under strong winds

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

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

463

464 Tail wind support along cyclone wakes

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

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

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

485

486 Chlorophyll A and wind conditions within and outside cyclone wakes

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/m³, on average) than elsewhere along their tracks. Wind conditions experienced were, however, not significantly different, both considering TWC (paired t-

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

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