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1 **Seabird morphology determines**
2 **operational wind speeds, tolerable maxima**
3 **and responses to extremes**

4
5 Elham Nourani*^{1,2} Kamran Safi^{1,2}, Sophie de Grissac^{3,4}, David J. Anderson⁵, Nik C. Cole^{6,15}, Adam
6 Fell⁷, David Grémillet^{8,9}, Emmanouil Lempidakis¹⁰, Miriam Lerma¹¹, Jennifer L. McKee⁵, Lorien
7 Pichegru¹², Pascal Provost¹³, Niels C. Rattenborg¹⁴, Peter G. Ryan⁹, Carlos D. Santos^{16,17,1}, Stefan
8 Schoombie⁹, Vikash Tatayah¹⁵, Henri Weimerskirch⁸, Martin Wikelski^{1,2,18}, Emily L. C. Shepard^{10,1}.

9
10 ¹ Department of Migration, Max Planck Institute of Animal Behavior, Am Obstberg 1, 78315 Radolfzell,
11 Germany.

12 ² Department of Biology, University of Konstanz, Universitätsstraße 10, 78464 Konstanz, Germany.

13 ³ Diomedea Science – Research & Scientific communication, 819 route de la Jars, 38 950 Quaix-en-Chartreuse,
14 France.

15 ⁴ France Energies Marines, Antenne Méditerranée, 38 rue Frédéric Jolliot-Curie, 13451 Marseille, France.

16 ⁵ Department of Biology, Wake Forest University, 1834 Wake Forest Rd, Winston-Salem, NC 27109, USA.

17 ⁶ Durrell Wildlife Conservation Trust, La Profonde Rue, JE3 5BP Jersey, Channel Islands.

18 ⁷ Biological and Environmental Sciences, University of Stirling, FK9 4LA Stirling, UK.

19 ⁸ CEFÉ, Univ Montpellier, CNRS, EPHE, IRD, 1919 route de Mende, 34293 Montpellier, France.

20 ⁹ FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town,
21 Rondebosch, 7701 Cape Town, South Africa.

22 ¹⁰ Department of Biosciences, Swansea University, SA1 8PP Swansea, UK.

23 ¹¹ Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany.

24 ¹² Institute for Coastal and Marine Research, Nelson Mandela University, 6031 Gqeberha, South Africa.

25 ¹³ Ligue pour la Protection des Oiseaux, Réserve Naturelle Nationale des Sept-Iles, 22560 Pleumeur Bodou,
26 France.

27 ¹⁴ Avian Sleep Group, Max Planck Institute for Ornithology, Eberhard-Gwinner-Straße, 82319 Starnberg,
28 Germany.

29 ¹⁵ Mauritian Wildlife Foundation, Grannum Road, 73418 Vacoas, Mauritius.

30 ¹⁶ Núcleo de Teoria e Pesquisa do Comportamento, Universidade Federal do Pará, R. Augusto Corrêa, 01 -
31 Guamá, PA, 66075-110, Belém, Brazil.

32 ¹⁷ CESAM - Centro de Estudos do Ambiente e do Mar, Faculdade de Ciências, Universidade de Lisboa,
33 Campo Grande 016, 1749-016 Lisboa, Portugal.

34 ¹⁸ Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Universitätsstraße 10,
35 78464 Konstanz, Germany.

36

37 ***Lead contact:** Elham Nourani

38 Email addresses: enourani@ab.mpg.de, mahle68@gmail.com

39 Twitter handle : @elham_nourani

40

41

42 **Author Contact**

43

44 Kamran Safi: ksafi@ab.mpg.de

45 Sophie de Grissac: s.degrissac@gmail.com

46 David J. Anderson: djanders@wfu.edu

47 Nik C. Cole: Nik.Cole@durrell.org

48 David Grémillet: david.gremillet@cefe.cnrs.fr

49 Emmanouil Lempidakis: emmanouil.lempidakis@swansea.ac.uk

- 50 Adam Fell: adam.fell@stir.ac.uk
- 51 Miriam Lerma: lerma@ftz-west.uni-kiel.de
- 52 Jennifer L. McKee: jenny.howard9@gmail.com
- 53 Lorien Pichegru: Lorien.Pichegru@mandela.ac.za
- 54 Pascal Provost: pascal.provost@lpo.fr
- 55 Niels C. Rattenborg: rattenborg@orn.mpg.de
- 56 Peter G. Ryan: pryan31@gmail.com
- 57 Carlos D. Santos: cdsantos@ab.mpg.de
- 58 Stefan Schoombie: schoombie@gmail.com
- 59 Vikash Tatayah: vtatayah@mauritian-wildlife.org
- 60 Henri Weimerskirch: Henri.WEIMERSKIRCH@cebc.cnrs.fr
- 61 Martin Wikelski: wikelski@ab.mpg.de
- 62 Emily Shepard: e.l.c.shepard@swansea.ac.uk

63 **Summary**

64 Storms can cause widespread seabird strandings and wrecking^{1,2,3,4,5}, yet little is known about the maximum wind
65 speeds that birds are able to tolerate or the conditions they avoid. We analyzed > 300,000 hours of tracking
66 data from 18 seabird species, including flapping and soaring fliers, to assess how flight morphology affects wind
67 selectivity, both at fine scales (hourly movement steps) and across the breeding season. We found no general
68 preference or avoidance of particular wind speeds within foraging tracks. This suggests seabird flight morphology
69 is adapted to a “wind niche”, with higher wing loading being selected for in windier environments. In support of
70 this, wing loading was positively related to the median wind speeds on the breeding grounds, as well as the maximum
71 wind speeds in which birds flew. Yet globally, the highest wind speeds occur in the tropics (in association with
72 tropical cyclones) where birds are morphologically adapted to low median wind speeds. Tropical species must
73 therefore show behavioral responses to extreme winds, including long-range avoidance of wind speeds that can
74 be twice their operable maxima. In contrast, procellariiformes flew in almost all wind speeds they encountered at a
75 seasonal scale. Despite this, we describe a small number of cases where albatrosses avoided strong winds at close-
76 range, including by flying into the eye of the storm. Extreme winds appear to pose context-dependent risks to
77 seabirds, and more information is needed on the factors that determine the hierarchy of risk, given the impact
78 of global change on storm intensity^{6,7}.

79

80

81 **Keywords:** Extreme weather events, storms, flight, wing loading, bio-logging

82

83

84 **Results**

85 The windscape largely determines seabirds’ flight costs. Seabirds should therefore adapt their behaviors
86 to reduce these costs in strong wind conditions. Wandering albatrosses, for example, travel in large loops
87 from Crozet Island, taking advantage of regional wind patterns to avoid head- winds⁸. Some seabirds reduce
88 exposure to strong winds by adjusting their flight distance to circumnavigate storms⁹. Even more widespread
89 is the tendency to decrease flight height when flying into a headwind^{10,9}. Here we investigated whether
90 flight morphology affects wind selectivity, both at fine scales (hourly movement steps) and across the breeding
91 season. We focused on preference or avoidance of wind speeds, rather than wind direction, as the latter
92 could be influenced by prey distribution, competition, and the need to return to a central place¹¹.

93 To understand the wind speeds seabirds are able to fly in and those they avoid, we analyzed 1,663 foraging
94 trips from 18 species of seabirds (Table S1), representing 326,960 hours of flight time. We compared the wind
95 speeds each bird encountered at every hourly segment (hereafter a step) along its foraging track with wind
96 speeds at 30 alternative steps that were available to the bird in space and time but were not used. Following
97 this step-selection approach (Figure S1), our dataset had a stratified structure, where each stratum was
98 composed of one observed step and its 30 alternative steps.

99 We chose not to proceed with the conditional logistic regressions commonly used to estimate step-
100 selection functions¹², as this disregards the outliers encountered by the birds in flight. Instead, we used null

101 modeling to compare the used and the maximum available wind speed within each step, and thereby identify the
102 rare wind-avoidance events (STAR Methods).

103 Birds experienced a wide range of wind speeds overall (Figure 1). However, the variation in wind speeds
104 available to them at any one point in time (calculated as the coefficient of variation for wind speed values
105 within each stratum) was generally low, with 90% of the strata showing variation lower than 11% (Figure S2),
106 and used wind speeds were not significantly different from the strongest speeds available to the birds (Figure
107 S3). Maximum wind speeds were avoided in only nine of the 93,104 strata, involving four species: Atlantic
108 yellow-nosed albatross, Wandering albatross, Sooty albatross, and Red-footed booby (Figure S3). In six of the
109 nine avoidance cases, birds avoided wind speeds that were within their population-specific flyable range of
110 wind speeds (Figure 1). The trips containing avoidance behavior indicated that the Atlantic yellow-nosed
111 and Wandering albatrosses were responding to storms by selecting the region of lower wind speeds by flying
112 towards and tracking the eye of the storm (Figure 2; Video S1).

113 We then investigated the factors that determined the maximum wind speeds encountered by each
114 species by comparing the encountered maxima with the general wind conditions within the species-specific
115 breeding distributions and seasons. We found that the maximum encountered wind speed was positively
116 correlated with the median ($adj R^2 = 0.83$, $p < 0.05$), but not the maximum ($adj R^2 = 0.05$, $p > 0.05$), available
117 wind speeds within the breeding range (Table S2). We tested whether morphological characteristics, which
118 largely define flight style, explained species-specific variation in the use of the windscape (Figure 3). Wing
119 loading explained 31% of variation in the strength of tolerable wind speed across species (Table S2). This result
120 was not influenced by temporal and spatial auto-correlation (STAR Methods), or by data quantity ($r = 0.15$, $p =$
121 0.53).

122

123 Discussion

124 Against our expectations, we found no general preference or avoidance of specific wind speeds across the
125 18 species studied at the hourly scale. The lack of a response to the general wind conditions, and the
126 overall low variation in wind speeds available, highlight that the seabird species in our study are adapted to the
127 “wind niche” that they occupy. Indeed, our results suggest that morphology is tightly linked to the wind regime
128 within a breeding distribution, with higher wing loading being advantageous for flight in windier environments.
129 This follows because airspeed increases with wing loading and birds must be able to fly faster than the wind if
130 they are to counter wind drift¹³. Yet while it has been suggested that flight style represents an important aspect
131 of seabird niche space¹⁴, the role of the windscape in shaping species distributions and diversity has only been
132 investigated for Procellariiformes¹⁵ (though see¹⁴). Our results therefore suggest that wind plays a wider role
133 in the biogeography of flight morphology and flight style through natural selection.

134 On a day-to-day basis, the strongest winds occurred in the Southern Ocean, an area frequently referred to
135 as the windiest place on earth⁸. However, while the Southern Ocean had the highest median wind speeds,
136 the overall maximum wind speeds were recorded in the tropical cyclone belt (Figure 1). As a result, the
137 seabirds that are exposed to the strongest global wind strengths (on a seasonal, rather than daily, basis)

138 are those that are morphologically adapted to low median wind speeds, in terms of their ability to counter
139 drift or land safely in strong winds. There should therefore be strong selection pressure for groups such as
140 tropicbirds to develop behavioral adaptations to avoid wind speeds that are some 8 - 9 times the speeds in
141 which they are able to fly. This is consistent with the avoidance of cyclones reported for frigatebirds and boobies,
142 which either remained on land or, depending on their age, made detours of hundreds of kilometers to
143 circumnavigate them⁹.

144 So why did our step selection approach detect so few instances of wind avoidance? This may be due to the
145 fine scale at which we examined wind speed selectivity (using step lengths of one hour). Given that average
146 airspeeds typically range from 10 to 18 m s⁻¹ in seabirds¹⁶, birds would need to select winds that were
147 significantly different to those available within a radius of some 40 – 65 km, for our approach to categorize the
148 behavior as avoidance. Yet adult Great frigatebirds responded to extreme cyclones (wind speed > 17 m s⁻¹) when
149 the storm eye was 250 km away⁹, and Black-naped terns (*Sterna sumatrana*) departed the colony when cyclones
150 (wind speed > 25 m s⁻¹) were 400 to > 2000 km away¹⁷. Indeed, it seems likely that the tropical seabirds in
151 this study showed similar long-range responses to extreme winds, or ceased flying altogether, given the
152 discrepancy between the maximum speeds available across the breeding distribution as a whole and those
153 experienced by birds in flight (Figure 1). The use of hourly step lengths may actually select for cases where birds
154 are able to operate very close to storm fronts, which could explain why we found the clearest cases of wind
155 avoidance in albatrosses, the most wind-adapted group.

156 The few instances where albatrosses did avoid extreme winds provide insight into the speeds and
157 scenarios when wind becomes costly or risky. We show that two species of albatross, including the Wandering
158 albatross, avoided gale force winds of 22 m s⁻¹ by flying into and tracking the eye of the storm (Figure 2).
159 Another instance, where an Atlantic yellow-nosed albatross briefly flew into the eye of a weaker storm (around
160 2014-11-18 21:00, see Video S1), was not identified as wind-avoidance, suggesting that this behavior may be
161 more common than our analyses suggest. Indeed, the same response has been identified in Streaked
162 shearwaters (*Calonectris leucomelas*)¹⁸, and is therefore used by species ranging in body mass from 0.5 to 12
163 kg. Flying towards and remaining within the eye of a storm could be an important part of the behavioral
164 repertoire of fast-flying, wind-adapted species, enabling them to modulate their exposure to unfavorable wind
165 vectors. This raises further interesting questions, such as why birds did not become entrained in the path of the
166 storm. However, understanding how precisely birds interact with the eye of the storm is likely to require wind
167 data at finer temporal resolution than that currently available for public use.

168 Overall, understanding the responses of animals to global change requires analysis of environmental
169 maxima and rare events. Although temperature maxima and minima are commonly used, e.g. for species
170 distribution modeling¹⁹, extreme wind conditions have not received the same attention. While the birds in
171 our study did not select their foraging trajectories in relation to local wind maxima or minima, tropical species
172 did appear to show larger-scale avoidance of extreme winds, as evident in the notable discrepancy between the
173 maximum wind speed they flew in and those available within their breeding distributions. As a result, the
174 maximum wind speeds that birds were recorded flying in provide new insight into the conditions that seabirds

175 with variable size and morphology are able to tolerate. The interspecific variation in these speeds, itself
176 predicted by wing loading, highlights that the definition of “extreme” wind speeds should be considered
177 relative to a given flight morphology, being linked to both flight speed and flight style.

178

179

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181

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194

195

196 **Author contributions**

197

198 ELCS conceived the study. EN designed the analyses with input from KS, ELCS, and SdG. DJA, NCC, AF, DG, ML,
199 JLM, LP, PP, NCR, PGR, CDS, SS, VT, HW, and MW contributed data. EN, SdG, and EL prepared the data for analysis.
200 EN analysed the data. EN and ELCS wrote the first draft of the manuscript. All authors commented on and
201 edited the manuscript drafts.

202

203

204 **Declaration of interests**

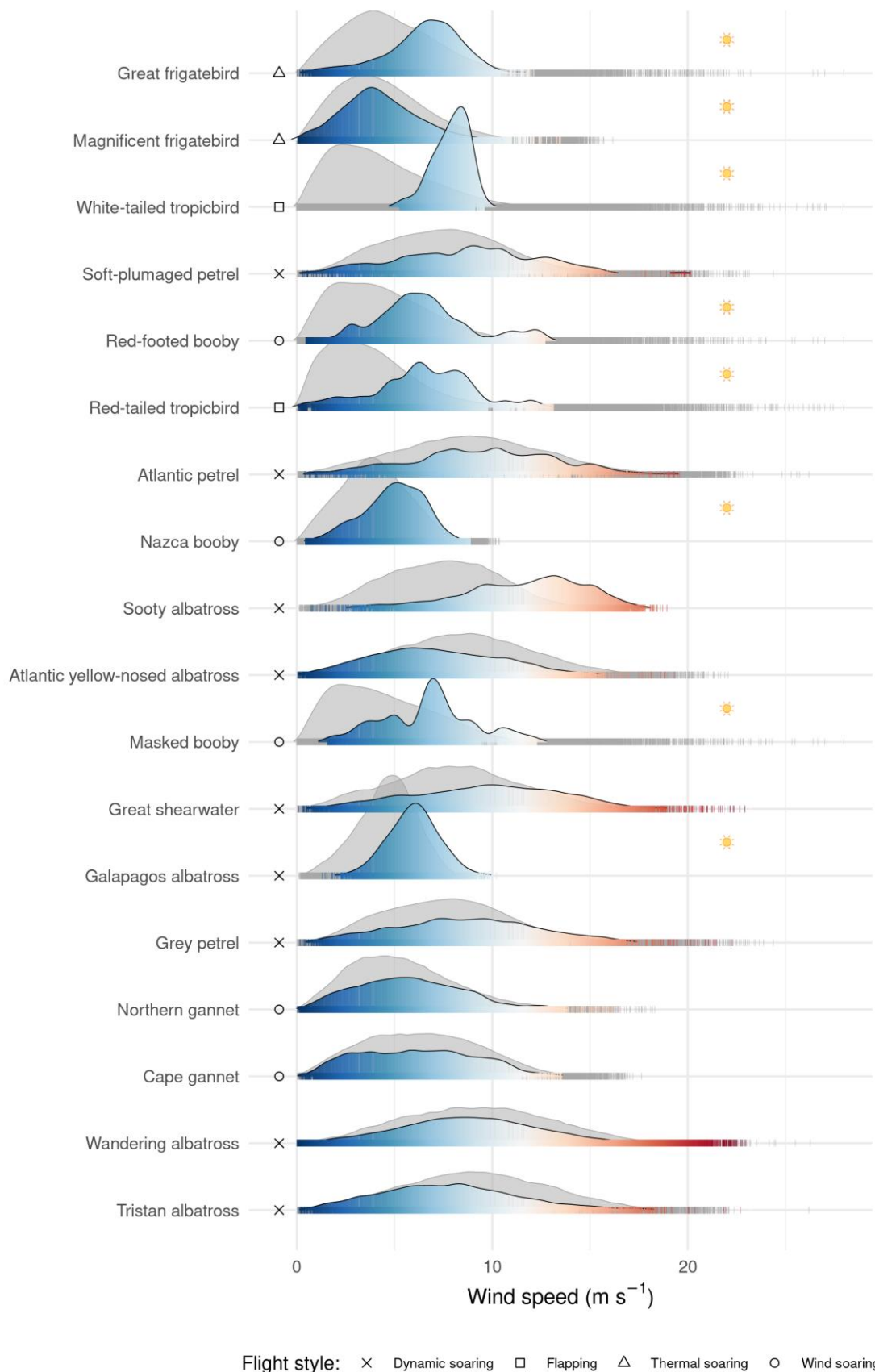
205

206 The authors declare no competing interests.

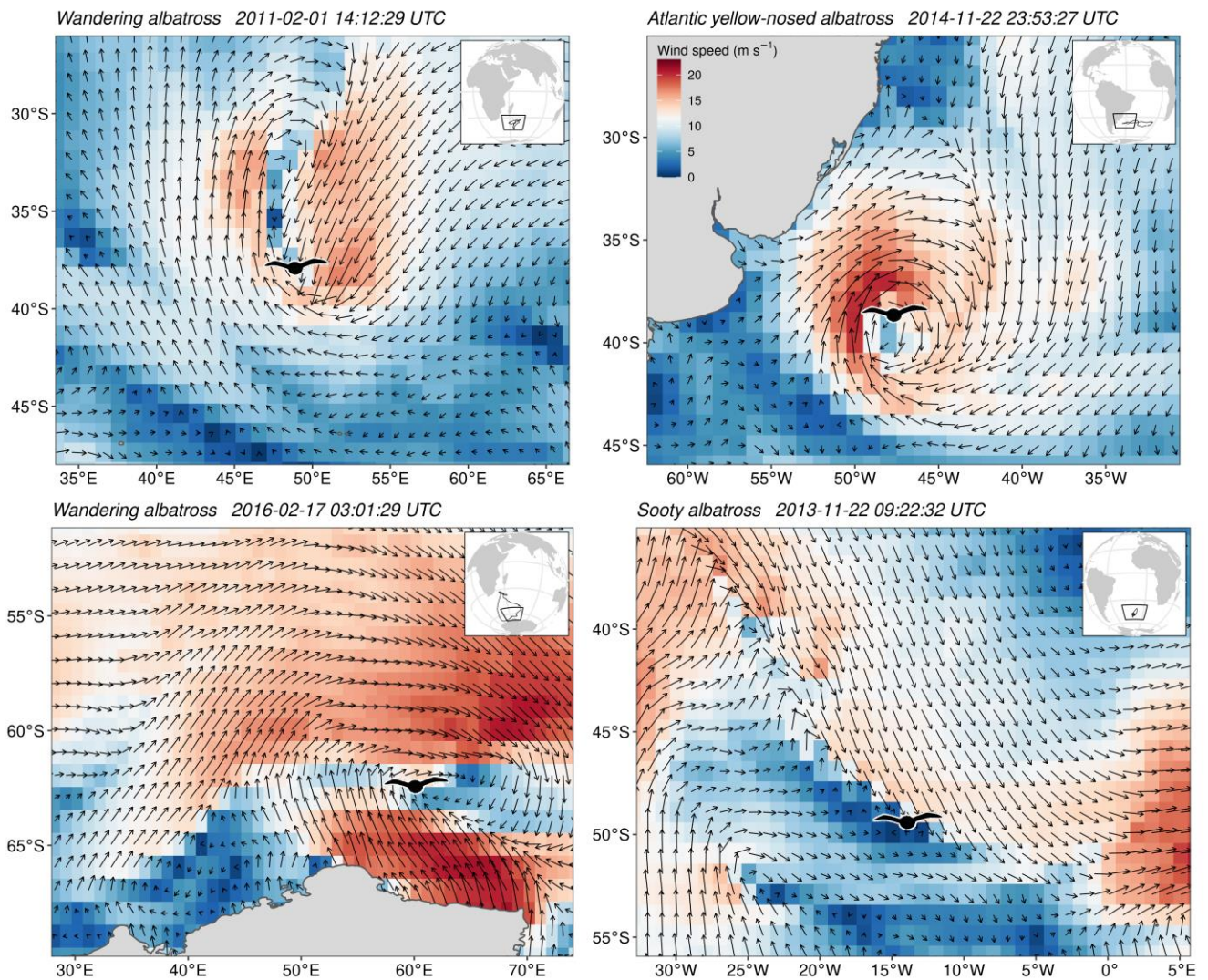
207

208

209 **Main-text figure/table legends**



210
 211 **Figure 1: Distribution of wind speeds.** Wind speeds experienced during foraging trips (in color. Colors
 212 correspond to wind speed, as in Figure 2) is compared to wind conditions across the entire breeding
 213 distribution and season over a 5-year period (in gray). Species are ordered by their wing loading, with the
 214 lowest wing loading at the top. Tropical species are indicated by a sun icon. See Table S1 for colony locations
 215 and wing loadings. See Figure S2 for coefficient of variation of wind speeds encountered by each species.



216

217 **Figure 2: Wind fields at four selected instances where birds avoided the strongest winds.** The location of the

218 bird at the time of avoidance of strongest available wind is shown. The full foraging trajectories are shown in the

219 plot insets. In the top two panels birds appear to avoid the strongest winds associated with cyclonic systems

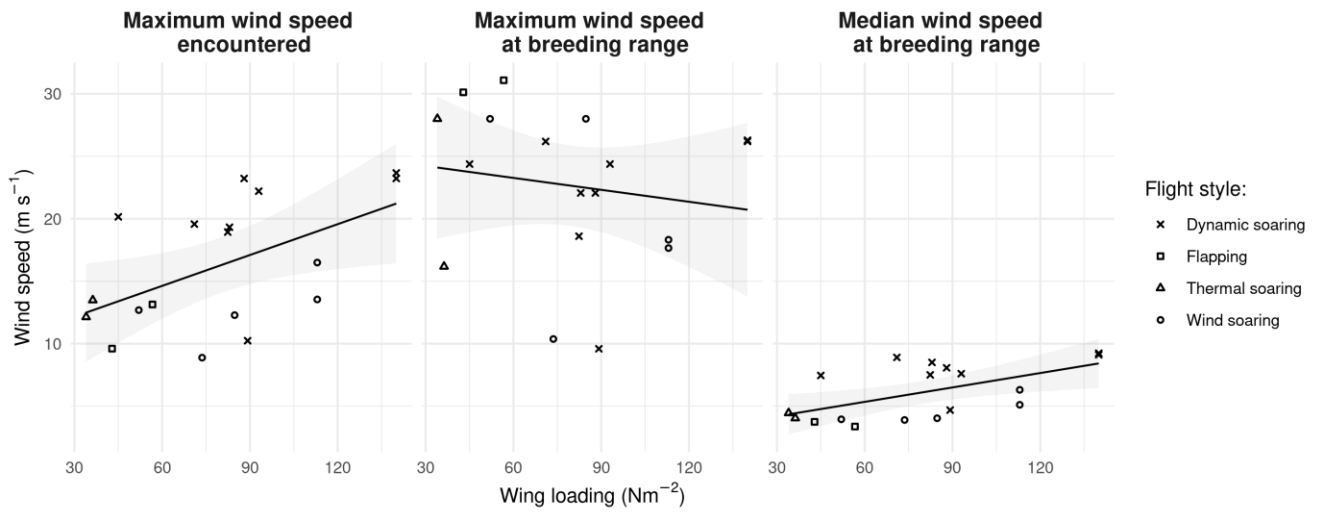
220 by tracking the low wind region in the eye of the storm (see also video S1). In the bottom two panels birds

221 operated along the edge of strong frontal systems, again selecting the region of lower wind speeds. See Figure

222 S3 for available and favored wind speed values.

223

224



225

226 **Figure 3: The relationship between wing loading and wind speed.** The maximum wind speed encountered by
 227 seabirds at the hourly scale was correlated with wing loading ($adj R^2 = 0.31, p < 0.05$). Wing loading was
 228 predicted by the median ($adj R^2 = 0.35, p < 0.05$), but not the maximum ($adj R^2 = -0.04, p = 0.64$) wind speeds
 229 within the breeding range, indicating that morphological adaptations are a response to the median wind
 230 conditions. Shaded areas show the 95% confidence intervals of the regression lines. See Table S2 for complete
 231 model summaries.

232 **STAR Methods**

233

234 **Resource availability**

235

236 *Lead contact*

237 Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead

238 contact, Elham Nourani (enourani@ab.mpg.de or mahle68@gmail.com).

239 *Materials availability*

240 This study did not generate new unique reagents.

241 *Data and code availability*

242 Annotated data are available via the Edmond repository "seabirds' wind niche"²⁰. R scripts are available via

243 https://github.com/mahle68/seabirds_storms_public²¹. Raw datasets are stored on Movebank or the Seabird

244 Tracking Database (as listed in Table S1).

245

246

247 **Experimental model and subject details**

248

249 All analysis was done on already-existing data collected for free-flying seabirds of the following

250 species:

251 1. Atlantic yellow-nosed albatross (*Thalassarche chlororhynchus*)

252 2. Galapagos albatross (aka. Waved albatross; *Phoebastria irrorata*)

253 3. Sooty albatross (*Phoebastria fusca*)

254 4. Tristan albatross (*Diomedea dabbenena*)

255 5. Wandering albatross (*Diomedea exulans*)

256 6. Atlantic petrel (*Pterodroma incerta*)

257 7. Grey petrel (*Procellaria cinerea*)

258 8. Soft-plumaged petrel (*Pterodroma mollis*)

259 9. Great shearwater (*Ardenna gravis*)

260 10. Cape gannet (*Morus capensis*)

261 11. Northern gannet (*Morus bassanus*)

262 12. Masked booby (*Sula dactylatra*)

263 13. Nazca booby (*Sula granti*)

264 14. Red-footed booby (*Sula sula*)

265 15. Great frigatebird (*Fregata minor*)

266 16. Magnificent frigatebird (*Fregata magnificens*)

267 17. Red-tailed tropicbird (*Phaethon rubricauda*)

268 18. White-tailed tropicbird (*Phaethon lepturus*)

269

270

271 **Method details**

272

273 **Bio-logging data**

274
275 We collected bio-logging data recorded using Platform Transmitter Terminals (PTTs) or GPS loggers for 18
276 seabird species (Table S1). These datasets were identified by searching Movebank (www.movebank.org)
277 and the Seabird Tracking Database (www.seabirdtracking.org). The species included in this study represent a
278 range of seabird flight styles (Table S1), including dynamic soaring (gaining energy by repeatedly crossing the
279 vertical gradient of wind velocity over the ocean²²; nine species of albatross, petrel, and shearwater), wind
280 soaring (regularly alternating flapping and gliding bouts to take advantage of the wind²³; five species of gannet
281 and booby), thermal soaring (soaring in circles on rising air columns and gliding down in the direction of travel²⁴;
282 two species of frigatebird), and obligate flapping fliers (two species of tropicbird). We focused on foraging
283 tracks of adult birds during the breeding season due to the availability of relatively high frequency tracking data,
284 which are scarce outside the breeding season. Diving seabirds such as alcids were not included in our study, as
285 their high wing loading could be selected for due to their use of wings for propulsion underwater and/or to
286 reduce buoyancy²⁵.

287 All data were filtered by speed to ensure that the position information represented periods of flight
288 (threshold of 2 - 3 km h⁻¹). To reduce auto-correlation and allow for comparisons between species, we sub-
289 sampled all data to a uniform temporal resolution of at least 1 hour (with tolerance of 15 minutes²⁶). In
290 the case of the Galapagos albatross (also known as Waved albatross), we used a 90 minute resolution, which
291 matched the original data frequency. Two species (Red-footed booby and Magnificent frigatebird) were
292 represented from two breeding colonies (Table S1). The Magnificent frigatebird dataset from Isla Contoy had
293 a low temporal resolution (median of 180 minutes) and was excluded from the random step generation
294 procedure (see below). We still report the strongest wind speed encountered by this population and include
295 it in the models for determining exposure to strong wind.

296 297 **Processing of bio-logging data**

298
299 We used a step-selection approach to prepare the data for analysis (Figure S1). This method allowed us
300 to compare the birds' use of the windscape during foraging trips to conditions that were available, but not
301 used. We considered every two consecutive points along a track as one step, each of them starting at point A
302 and ending at point B. For each of these observed steps, we randomly generated 30 alternative steps, each of
303 which originated in the same place, point A of the observed step, but went to a different location in space,
304 with the same timestamp, as the observed step did. Thus, for each step, we randomly drew 30 values from the
305 distribution of step lengths (Gamma distribution) and turning angles (von Mises distribution) fitted to the
306 empirical data for each species to construct the steps originating in each of the observed location A, but going
307 to 30 alternative B locations. As such, our dataset had a stratified structure, where 30 alternative steps were
308 matched to one observed step per stratum.

309 For each point in the dataset, we extracted eastward (u) and northward (v) components of wind (at 10 m
310 above surface) from the European Center for Medium-Range Weather Forecast (ECMWF; www.ecmwf.int) ERA5
311 re-analysis database (temporal and spatial resolution of 1 hour and 30 km, respectively). Annotations were
312 done using the ENV-Data track annotation service²⁷ provided by Movebank. We selected bi-linear

313 interpolation for all variables and calculated wind speed using the u and v components of the wind. For each
314 species, we obtained wing loading and aspect ratio from the literature (Table S1).

315 Preliminary inspection of the largest dataset (Wandering albatross) revealed that the response to extreme
316 winds appeared similar for this species irrespective of whether the step length was set to 1, 2, 4, or 6 hours.

317

318 **Wind conditions at species-specific breeding distributions**

319

320 To understand seabirds' wind selectivity with regards to the general conditions in their breeding range, we
321 downloaded the eastward and northward components of the wind for the species-specific breeding
322 distributions and seasons. Wind data were obtained for a five year period (2017-2021) from ERA5 for each
323 species breeding range, as given in the BirdLife International database (<http://datazone.birdlife.org>). We then
324 calculated the maximum and median wind speeds within each species' breeding distribution and season.

325

326 **Quantification and statistical analysis**

327

328 **Testing for avoidance of strong wind**

329

330 We used a null modeling technique to test whether seabirds avoided strong winds when foraging at sea. We
331 did not make any assumptions about what wind speeds were considered strong or extreme. Instead, for
332 each set of used and 30 alternative steps (i.e., a stratum), we compared the strongest available wind speed
333 to the wind speed that the individual used. Each stratum was therefore considered to be one sampling
334 unit. Our null hypothesis was that, within each stratum, there was no avoidance of the strongest available
335 wind. Our alternative hypothesis was that the strongest wind available in the stratum was avoided. We calculated
336 a test statistic within each stratum: the difference between the maximum wind speed available and the wind
337 speed at the observed point. To create a null dataset, we grouped the data by species, year, and stratum, and
338 shuffled the wind speed values associated with each row of data within each of these groups. We then
339 calculated the same test statistic within the randomized strata. We repeated the randomization 1,000 times.
340 Given our one-sided alternative hypothesis, we calculated significance as the fraction of random test statistics
341 that were greater than or equal to the observed test statistic.

342

343 **Determinants of exposure to strong wind**

344

345 We used linear models to investigate whether morphology determined the exposure of seabird species to
346 strong wind conditions. Due to the positive correlation between wing loading and aspect ratio ($r = 0.60$, $p <$
347 0.05), we included wing loading as the sole predictor in our linear models.

348 We extracted the maximum wind speed experienced by each species population from the annotated bio-
349 logging dataset (one-hourly resolution). Each population (i.e., species-colony combination) was considered as
350 one sampling unit. We predicted maximum wind as a function of wing loading and checked the model residuals
351 for spatial and temporal auto-correlation that could be related to colony location and timing of breeding
352 (estimated as the median month of the breeding season) following Korner et al.²⁸.

353 The amount of data varied for each species. To test whether the maximum wind speed experienced by

354 different species was affected by the amount of flight data in our dataset, we estimated the correlation between
355 these.

356 We also investigated whether maximum wind speed experienced by each species was determined by the
357 wind conditions during the breeding season as a whole. For this, we ran linear models predicting maximum
358 encountered wind with the maximum and median wind speed at the breeding distribution.

359 **Legends for supplemental Excel tables, videos, or dataset files**

360

361 **Video S1: An Atlantic yellow-nosed albatross flies into the eye of the storm, related to Figure 2.** The bird
362 (indicated by an albatross silhouette) was identified to be avoiding strong winds at 2014-11-22 23:53:27 UTC.
363 However, it also briefly flew into the eye of a weaker storm around 2014-11-18 21:00 UTC. This instance
364 was not identified as wind-avoidance in our study, suggesting that this behavior may be more common than
365 our analysis suggests. Flying towards and remaining within the eye of a storm could be an important part of
366 the behavioral repertoire of fast-flying, wind-adapted species, enabling them to modulate their exposure to
367 unfavorable winds.

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