Extreme tolerable winds for seabirds are determined by morphology

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Summary

Storms can cause widespread seabird strandings and wrecking[1,2,3,4,5], yet little is known about the maximum wind speeds that birds are able to tolerate or the conditions they avoid. We analyzed $>$ 300,000 hours of tracking data from 18 seabird species, including flapping and soaring fliers, to quantify the wind speeds used during the breeding season in relation to those available. We found no general preference nor avoidance of particular wind speeds, indicating that wind did not strongly shape decision-making processes for central place foragers. Instead, we suggest that seabirds are adapted to a "wind niche", where species with higher wing loading are selected for a life in windier environments. In support of this, wing loading was positively related to the median wind speeds on the breeding grounds and the maximum wind speeds in which birds flew. Importantly, the highest wind speeds occurred in the tropics (in association with tropical cyclones) where birds are morphologically adapted to low median wind speeds. These species should therefore show behavioral responses to extreme winds, which likely include long-range avoidance. We also discovered a very small number of instances where albatrosses avoided strong winds at close-range, demonstrating that even the most wind-adapted birds occasionally avoid extreme speeds. Extreme winds appear to pose context-dependent risks to seabirds, and there is a need for more information on the factors that determine the hierarchy of risk, given the impact of global change on storm intensity[6,7].

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

Results

The windscape largely determines seabirds' flight costs. Seabirds should therefore adapt their behaviors to reduce these costs in strong wind conditions. Wandering albatrosses, for example, travel in large loops from Crozet Island, apparently taking advantage of regional wind patterns to avoid head winds[8]. Some auks reduce exposure to strong winds by adjusting their flight distance[9,10]. Even more widespread is the tendency to decrease flight height when flying into a headwind[11,10]. Here we investigated whether the local wind field shapes route-choice in breeding seabirds. We focused on preference or avoidance of wind speeds, rather than wind direction, which could be influenced by prey distribution, competition, and the need to return to a central place[12].

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

We chose not to proceed with the conditional logistic regressions commonly used to estimate step-selection functions[13], as this disregards the outliers encountered by the birds in flight. Instead, we used null modeling to compare the used and the maximum available wind speed within each step, and thereby identify the rare wind-avoidance events.

The birds experienced a wide range of wind speeds overall (Fig. 2). However, the variation in wind speeds available to them at any one point in time (calculated as the coefficient of variation for wind speed values within each stratum) was generally low, with 90% of the strata showing variation lower than 11% (Fig. S1). We thus found that the used wind speeds were not significantly different from the strongest speeds available to the birds (Fig. S2). Maximum wind speeds were avoided in only nine of the 93,104 strata, involving four species: Atlantic yellow-nosed albatross, Wandering albatross, Sooty albatross, and Red-footed booby (Fig. S3). In six of the nine cases where birds avoided the wind speed maxima, birds avoided wind speeds that were within their population-specific flyable range of wind speeds (Fig. 2). The trips containing avoidance behavior indicated that the Atlantic yellow-nosed and Wandering albatrosses were responding to storms by selecting the region of lower wind speeds, i.e. by flying towards and tracking the eye of the storm (Fig. 3; Supplementary video).

We then investigated the factors that determine the maximum wind speeds encountered by each species. We compared the encountered maxima with the general wind conditions within the species-specific breeding distribution ranges. We found that the maximum encountered wind speed was positively correlated with the median ($adj\ R^2 = 0.84$, $p < 0.05$) but not the maximum wind speeds that occurred in the breeding range (Fig. 4). We tested whether morphological characteristics, which largely define flight style, explained species-specific variation in the use of the windscape (Fig. 4). Wing loading explained 31% of variation in the strength of tolerable wind speed across species (Tables S2). This result was neither influenced by temporal and spatial auto-correlation, nor by data quantity ($r = 0.15$, $p = 0.53$).

Discussion

Against our expectations, we found no general preference or avoidance of specific wind speeds across the 18 species studied (at the hourly scale). The lack of a response to the general wind conditions, and the overall low variation in wind speeds available, highlight that the seabird species we investigated are adapted to the “wind niche” that they occupy. Indeed, our results suggest that morphology is tightly linked to the wind regime within a breeding distribution, with higher wing loading being advantageous for flight in windier environments. This follows because airspeed increases with wing loading and birds must be able to fly faster than the wind if they are to counter wind drift[14]. Yet while it has been suggested that flight style represents an important aspect of seabird niche space[15],

the role of the windscape in shaping species distributions and diversity has only been investigated for Procellariiformes[16] (though see[15]). Our results suggest wind therefore plays a wider role in the biogeography of flight morphology and flight style through natural selection and/or spatial filtering (Fig. 2).

On a day-to-day basis, the strongest winds occurred in the Southern Ocean, an area frequently referred to as the windiest place on earth[8]. However, while the Southern Ocean had the highest median wind speeds, the maximum wind speeds were recorded in the tropical cyclone belt (Fig. 2). As a result, the seabirds that are exposed to the strongest global wind strengths are those that are morphologically adapted to low median wind speeds, in terms of their ability to counter drift or land safely in strong winds. There should therefore be strong selection pressure for groups such as tropicbirds for behavioral adaptations to avoid wind speeds that are some 8 - 9 times what they are able to fly in. This is consistent with the avoidance of cyclones reported for frigatebirds and boobies, which either remained on land or, depending on their age, made detours of hundreds of kilometers to circumnavigate them[10].

So why did our step selection approach detect so few instances of wind avoidance? This may be due to the fine scale at which we examined wind speed selectivity (using step lengths of one hour). Given that average airspeeds typically range from 10 to 18 m s^{-1} in seabirds[17], birds would need to select winds that were significantly different to those available within a radius of some 40 – 65 km, for our approach to categorize the behavior as avoidance. Yet adult Great frigatebirds responded to extreme cyclones (wind speed > 17 m s^{-1}) when the storm eye was 250 km away[10], and Black-naped terns (*Sterna sumatrana*) departed the colony when cyclones (wind speed > 25 m s^{-1}) were 400 to > 2000 km away[18]. Indeed, it seems likely that tropical seabirds in this study showed similar long-range responses to extreme winds, or ceased flying altogether, given the discrepancy between the maximum speeds available across the breeding distribution as a whole and those experienced by birds in flight (Fig. 2). The use of hourly step lengths may actually select for cases where birds are able to operate very close to storm fronts, which could explain why we found the clearest cases of wind avoidance in albatrosses, the most wind adapted group.

The few instances where albatrosses did avoid extreme winds provide insight into the speeds and scenarios when wind becomes costly or risky. We show that two species of albatross, including the Wandering albatross, avoided gale force winds of 22 m s^{-1} by flying into and tracking the eye of the storm (Fig. 3). Another instance, where an Atlantic yellow-nosed albatross briefly flew into the eye of a weaker storm (around 2014-11-18 21:00, see Supplementary video), was not identified as wind-avoidance, suggesting that this behavior may be more common than our analyses suggest. Indeed, the same response has been identified in Streaked shearwaters (*Calonectris leucomelas*)[19], and is therefore used by species ranging in body mass from 0.5 to 12 kg. Flying towards and remaining

within the eye of a storm could be an important part of the behavioral repertoire of fast-flying, wind-adapted species, enabling them to modulate their exposure to unfavorable winds. This raises further interesting questions, such as why birds did not become entrained in the path of the storm. However, understanding how precisely birds interact with the eye of the storm is likely to require wind data at finer temporal resolution than what is currently available for public use.

Overall, understanding the responses of animals to global change requires analysis of environmental maxima and rare events. Although temperature maxima and minima are commonly used, e.g. in species distribution modeling[20], extreme wind conditions have not received the same attention. While the birds in our study did not select their foraging trajectories in relation to local wind maxima or minima, tropical species did appear to show larger-scale avoidance of extreme winds, as evident in the notable discrepancy between the maximum wind speed they flew in and those available within their breeding distributions. As a result, the maximum wind speeds that birds were recorded flying in provide new insight into the conditions that seabirds with variable size and morphology are able to tolerate (although groups such as auks, which have the highest wing loading, are not represented). The interspecific variation in these speeds, itself predicted by wing loading, highlights that the definition of "extreme" wind speeds should be considered relative to a given flight morphology, being linked to both flight speed and flight style.

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Author contributions

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

Declaration of interests

The authors declare no competing interests.

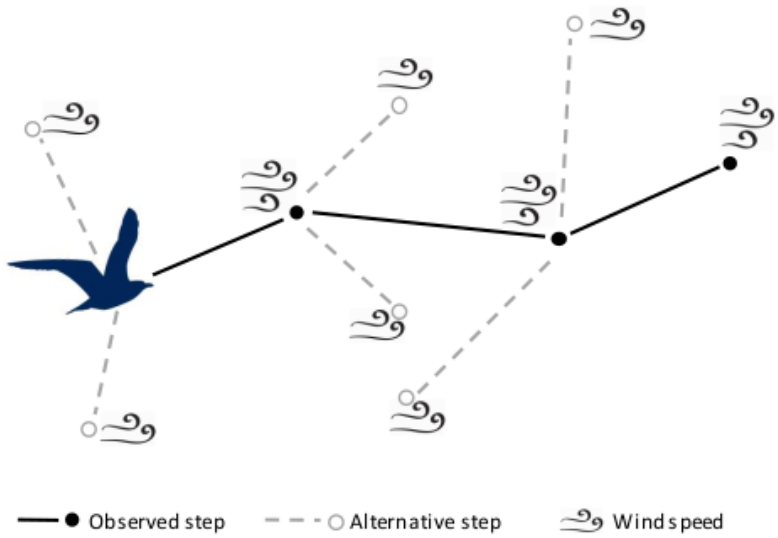

Figure 1: Schematic example of the step-selection approach used in this study. Each pair of consecutive locations is considered as one observed step. Each observed step is associated with a number of alternative steps (2 in this example), creating one stratum. The location of alternative steps is determined by randomly selecting a step length and a turn angle from the gamma distribution of step lengths and the von Mises distribution of turn angles observed for each species. The favored wind speed within each stratum is then compared to the maximum available wind speed within the stratum. In this example the bird favored the strongest available wind in all the strata.

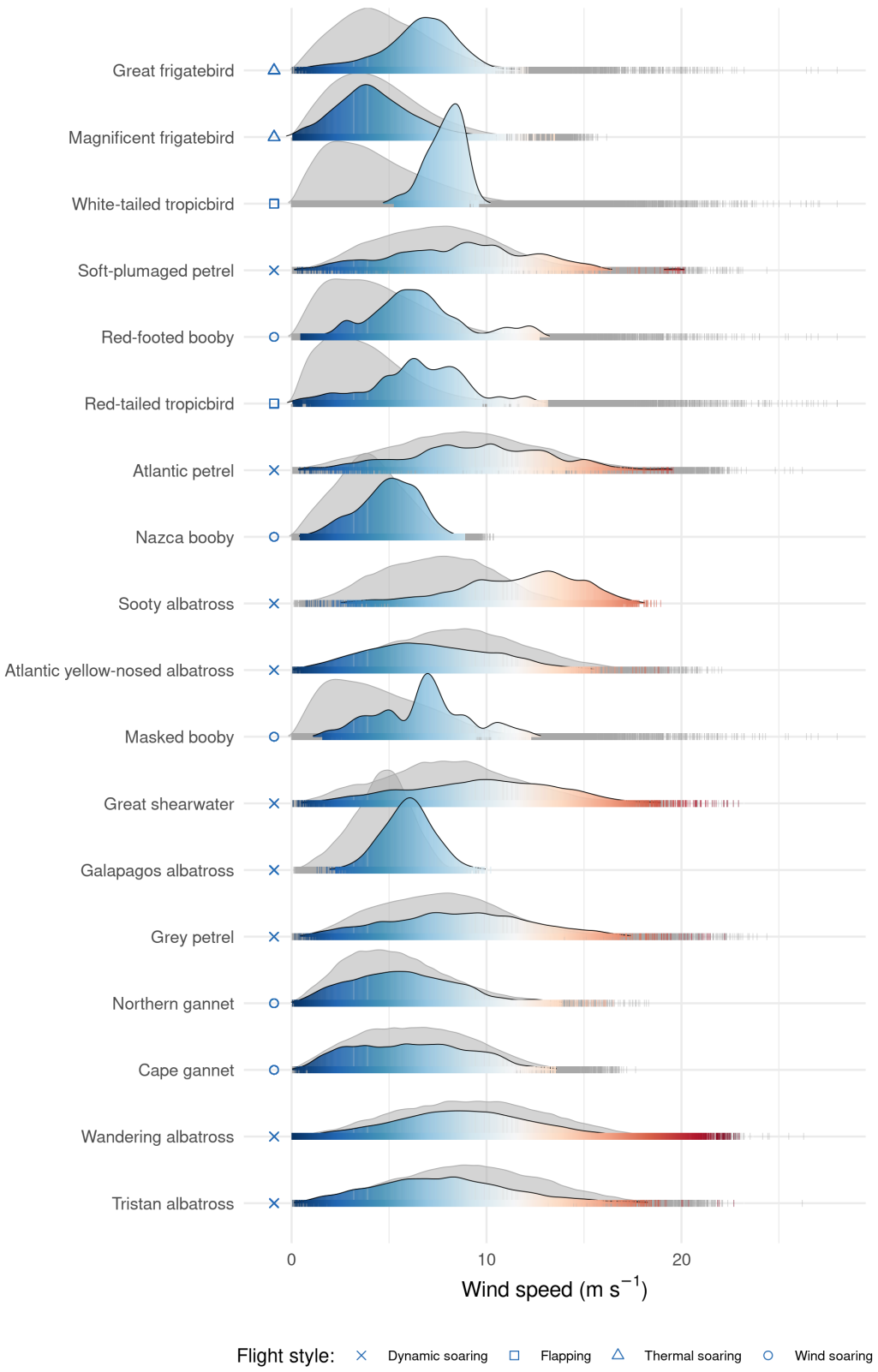

Figure 2: Distribution of wind speeds experienced during foraging trips (in color. Colors correspond to those in Fig. 3) compared to wind conditions across the entire breeding distribution for each species (in gray). Vertical bars show the raw data points for wind speeds encountered by the birds (in color) and wind speeds available across the breeding distribution over a 5-year period (gray). Species are ordered by their wing loading (Table S1), with the lowest wing loading at the top.

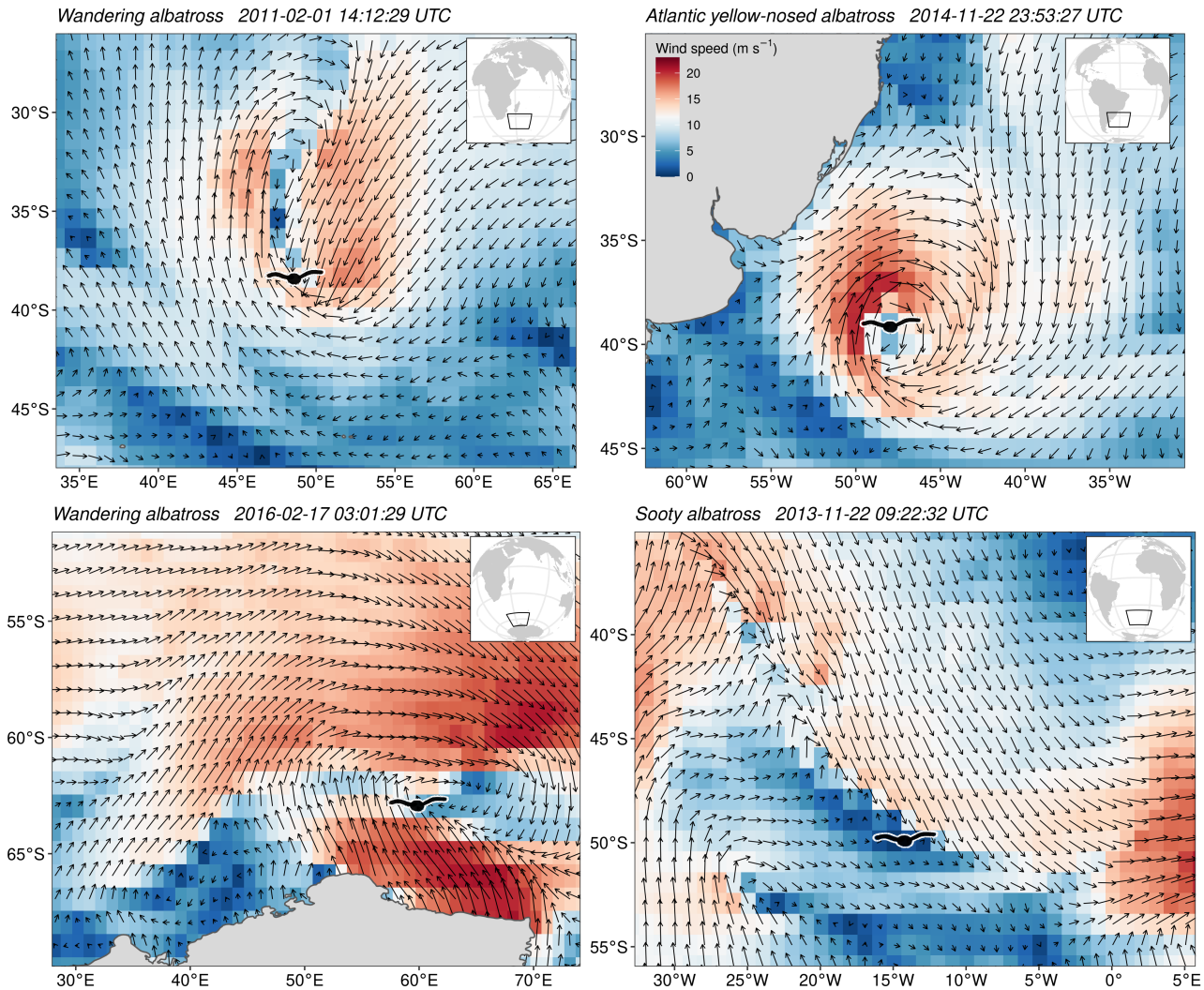

Figure 3: Wind fields at four selected instances where birds (indicated by an albatross silhouette) avoided the strongest winds. In the top two panels birds appear to avoid the strongest winds associated with cyclonic systems by tracking the low wind region in the eye of the storm. In the bottom two panels birds operated along the edge of strong frontal systems, again selecting the region of lower wind speeds.

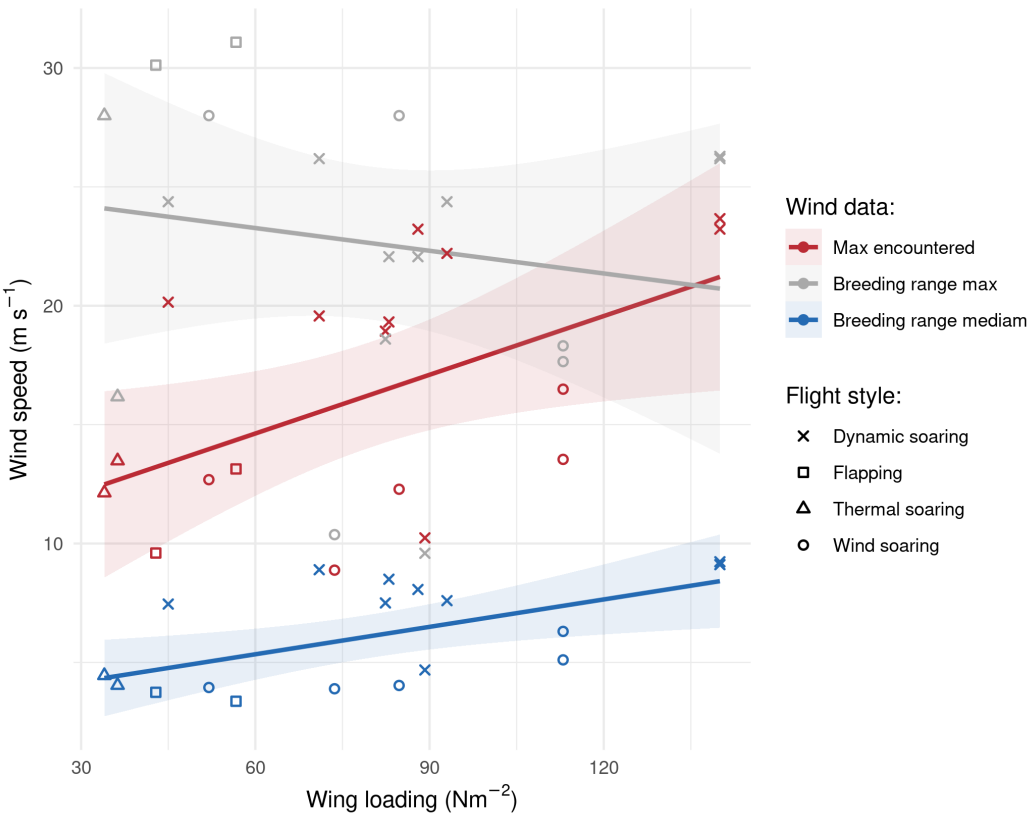

Figure 4: The relationship between wing loading and the maximum wind speed encountered by each species (red). This is compared with the overall median (blue) and maximum (gray) wind speeds at the species-specific breeding distribution. Shaded areas show the 95% Confidence Intervals of the regression lines. Wing loading can be 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 conditions at the breeding distribution, indicating that morphological adaptations are a response to the median wind conditions.

STAR Methods

Resource availability

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Elham Nourani (enourani@ab.mpg.de or mahle68@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Annotated data necessary for replicating the results of the study will be available via an Edmond repository (*https://edmond.mpdl.mpg.de/*) upon acceptance of the manuscript. Raw datasets are available on Movebank or the Seabird Tracking Database (as listed in Table S1). R scripts are available on *https://github.com/mahle68/seabirds_storms_public*. The corresponding DOIs for Edmond and Github repositories will be generated and reported here once the manuscript is accepted for publication.

Experimental model and subject details

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

1. Atlantic yellow-nosed albatross (*Thalassarche chlororhnchosy*)
2. Galapagos albatross (aka. Waved albatross; *Phoebastria irrorata*)
3. Sooty albatross (*Phoebetria fusca*)
4. Tristan albatross (*Diomedea dabbenena*)
5. Wandering albatross (*Diomedea exulans*)
6. Atlantic petrel (*Pterodroma incerta*)
7. Grey petrel (*Procellaria cinerea*)
8. Soft-plumaged petrel (*Pterodroma mollis*)
9. Great shearwater (*Ardenna gravis*)
10. Cape gannet (*Morus capensis*)
11. Northern gannet (*Morus bassanus*)

12. Masked booby (*Sula dactylatra*)
13. Nazca booby (*Sula granti*)
14. Red-footed booby (*Sula sula*)
15. Great frigatebird (*Fregata minor*)
16. Magnificent frigatebird (*Fregata magnificens*)
17. Red-tailed tropicbird (*Phaethon rubricauda*)
18. White-tailed tropicbird (*Phaethon lepturus*)

Method details

Bio-logging data

We collected bio-logging data recorded using Platform Transmitter Terminals (PTTs) or GPS loggers for 18 seabird species (Table S1). These datasets were identified by searching Movebank (*www.movebank.org*) and the Seabird Tracking Database (*www.seabirdtracking.org*). The species included in this study represent a range of seabird flight styles (Table S1), including dynamic soaring (gaining energy by repeatedly crossing the vertical gradient of wind velocity over the ocean[21]; nine species of albatross, petrel, and shearwater), wind soaring (regularly alternating flapping and gliding bouts to take advantage of the wind[22]; five species of gannet and booby), thermal soaring (soaring in circles on rising air columns and gliding down in the direction of travel[23]; two species of frigatebird), and obligate flapping fliers (two species of tropicbird), although notably data from alcids were not included. We focused on foraging tracks of adult birds during the breeding season due to the availability of relatively high frequency tracking data, which are scarce outside the breeding season.

All data were filtered by speed to ensure that the position information represented periods of flight (threshold of 2-3 km h^{-1}). To reduce auto-correlation and allow for comparisons between species, we sub-sampled all data to a uniform temporal resolution of at least 1 hour (with tolerance of 15 minutes[24]). In the case of the Galapagos albatross (also known as Waved albatross), we used a 90 minute resolution, which matched the original data frequency. Two species (Red-footed booby and Magnificent frigatebird) were represented from two breeding colonies. The Magnificent frigatebird dataset from Isla Contoy had a low temporal resolution (median of 180 minutes) and was excluded from the random step generation procedure (see below). We still report the strongest wind speed encountered by this population and include it in the model for determining exposure to strong wind.

Processing of bio-logging data

We used a step-selection approach to prepare the data for analysis. This method allowed us to compare the birds' use of the windscape during foraging trips to conditions that were available,

but not used. We considered every two consecutive points along a track as one step, each of them starting at point A and ending at point B. For each of these observed steps, we randomly generated 30 alternative steps, each of which originated in the same place, point A of the observed step, but went to a different location in space within the same time period as the observed step did. Thus, for each step, we randomly drew 30 values from the distribution of step lengths (Gamma distribution) and turning angles (von Mises distribution) fitted to the empirical data for each species to construct the steps originating in each of the observed location A, but going to 30 alternative B locations. As such, our dataset had a stratified structure, where 30 alternative steps were matched to one observed step per stratum.

For each point in the dataset, we extracted eastward (u) and northward (v) components of wind (at 10 m above surface) from the European Center for Medium-Range Weather Forecast (ECMWF; *www.ecmwf.int*) ERA5 re-analysis database (temporal and spatial resolution of 1 hour and 30 km, respectively). Annotations were done using the ENV-Data track annotation service[25] provided by Movebank. We selected bi-linear interpolation for all variables and calculated wind speed using the u and v components of the wind. For each species, we obtained wing loading and aspect ratio from the literature (Table S1).

Preliminary inspection of the largest dataset (Wandering albatross) revealed that the response to extreme winds appeared similar for this species irrespective of whether the step length was set to 1, 2, 4, or 6 hours (Fig. S4).

Wind conditions at species-specific breeding distributions

To have a better understanding of how often different species encounter "extremes" on their breeding grounds, we downloaded the eastward and northward components of the wind for the species-specific breeding distributions and seasons. Data were obtained for a five year period (2017-2021) from ERA5. We then calculated the maximum and median wind speeds within each species' breeding distribution.

Testing for avoidance of strong wind

We used a randomization technique to test whether seabirds avoided strong winds when foraging at sea. We did not make any assumptions about what wind speeds were considered strong or extreme. Instead, for each set of used and 30 alternative steps (i.e., a stratum), we compared the strongest available wind speed to the wind speed that the individual used. Each stratum was therefore considered to be one sampling unit. Our null hypothesis was that, within each stratum, there was no avoidance of the strongest available wind. Our alternative hypothesis was that the strongest wind available in the stratum was avoided. We calculated a test statistic within each stratum: the difference

between the maximum wind speed available and the wind speed at the observed point. To create a null dataset, we grouped the data by species, year, and stratum, and shuffled the wind speed values associated with each row of data within each of these groups. We then calculated the same test statistic within the randomized strata. We repeated the randomization 1,000 times. Given our one-sided alternative hypothesis, we calculated significance as the fraction of random test statistics that were greater than or equal to the observed test statistic.

Determinants of exposure to strong wind

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

We extracted the maximum wind speed experienced by each species population from the annotated bio-logging dataset (one-hourly resolution). Each population (i.e., species-colony combination) was considered as one sampling unit. We predicted maximum wind as a function of wing loading and checked the model residuals for spatial and temporal auto-correlation that could be related to colony location and timing of breeding (estimated as the median month of the breeding season) following Korner et al.[26].

The amount of data varied for each species. To test whether the maximum wind speed experienced by different species was affected by the amount of flight data in our dataset, we estimated the correlation between these.

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

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Supplementary Video

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

Supplementary Figures

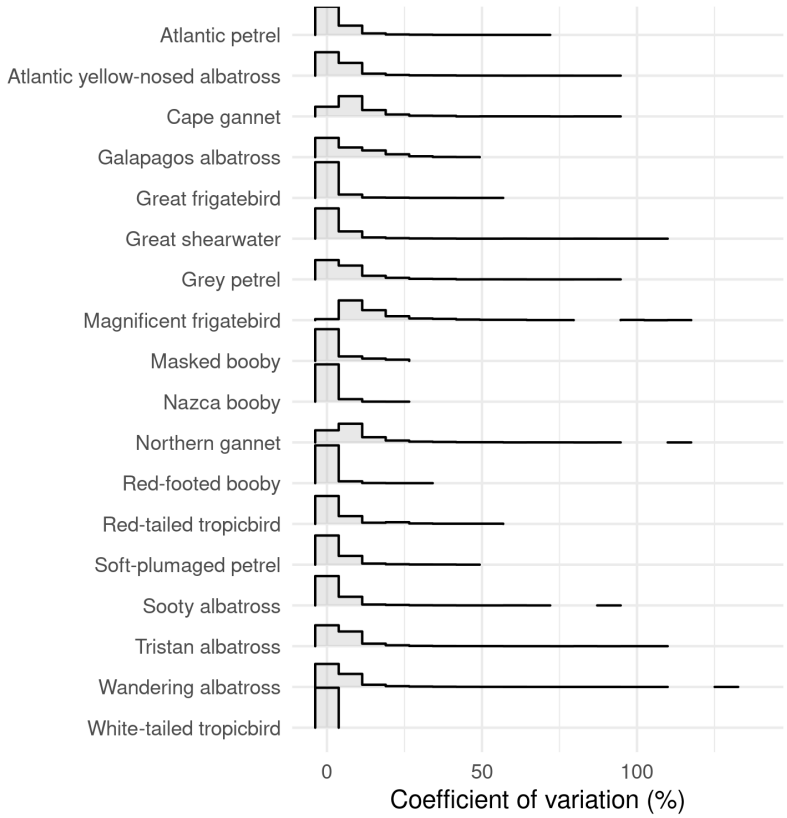

Figure S1: Distribution of coefficient of variation estimated for wind speed within each stratum for each species. Values exceeding 100% indicate higher standard deviation than the mean.

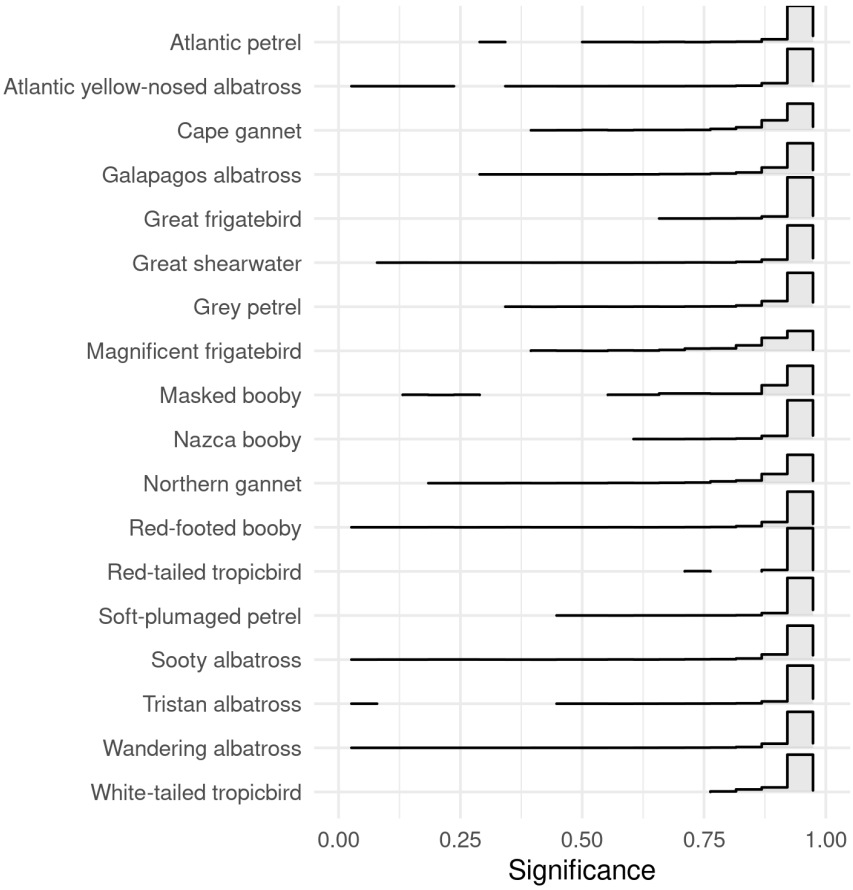

Figure S2: Significance values for randomization tests performed on the stratified dataset to test for avoidance of strong wind. The null hypothesis was accepted in the majority of strata: seabirds did not avoid strong winds. In fact, significant values of 1 indicate that the bird used the maximum wind speed available.

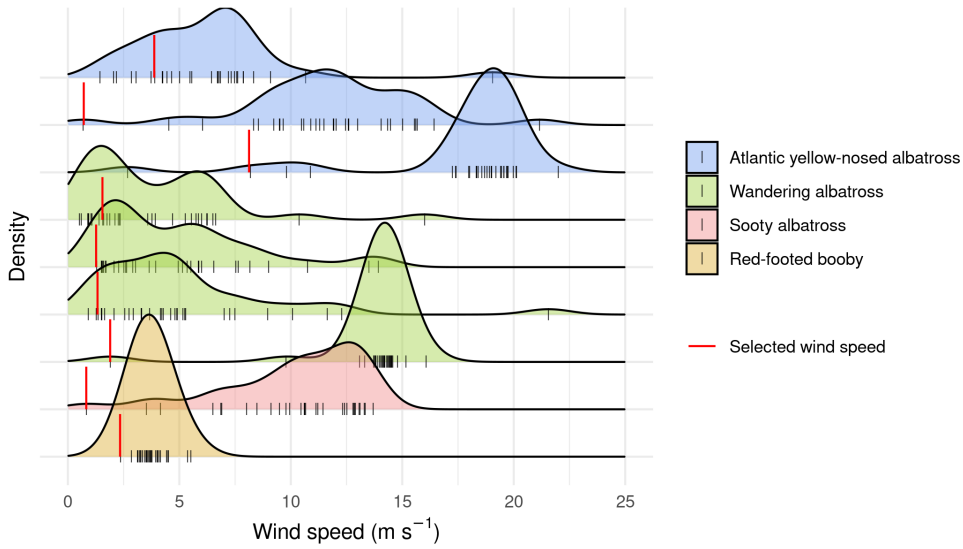

Figure S3: Distribution of available wind speed at the strata where strong wind was avoided. Wandering albatrosses sometimes avoided wind speeds that were well within their normal operational range (14, 15, and 16 m s^{-1}). This could either be because individual trajectories were driven by factors other than the wind field in these instances, or because birds chose to select/avoid wind conditions based on the direction rather than speed alone, for instance to enable the efficient exploitation of cross winds.

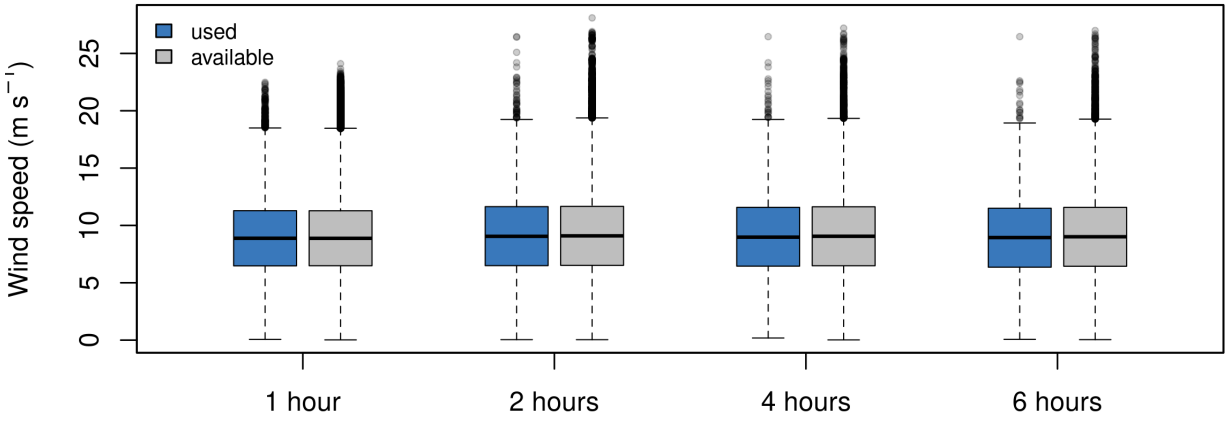

Figure S4: Distribution of wind speed (m s^{-1}) at used and available locations along the wandering albatross foraging tracks for step lengths set to 1, 2, 4, and 6 hours.