Extreme tolerable winds for seabirds are determined by morphology

Elham Nourani*[1,2] Kamran Safi[1,2], Sophie de Grissac[3,4], David J. Anderson[5], Nik C. Cole[6,15], Adam Fell[7], David Grémillet[8,9], Miriam Lerma[10], Jennifer L. McKee[5], Lorien Pichegru[11], Pascal Provost[12], Niels C. Rattenborg[13], Peter G. Ryan[9], Carlos D. Santos[14,1], Stefan Schoombie[9], Vikash Tatayah[15], Henri Weimerskirch[8], Martin Wikelski[1,2,16], Emily L. C. Shepard[17,1].

[1] Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany.

[2] Department of Biology, University of Konstanz, Konstanz, Germany.

[3] Diomedea Science – Research & Scientific communication, Quaix-en-Chartreuse, France.

[4] France Energies Marines, Antenne Méditerranée, Marseille, France.

[5] Department of Biology, Wake Forest University, Winston-Salem, NC, USA.

[6] Durrell Wildlife Conservation Trust, Jersey, Channel Islands.

[7] Biological and Environmental Sciences, University of Stirling, Stirling, UK.

[8] Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 CNRS/La Rochelle Univ, France.

[9] FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, South Africa.

[10] Research and Technology Centre (FTZ), University of Kiel, Kiel, Germany.

[11] Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha, South Africa.

[12] Ligue pour la Protection des Oiseaux, Réserve Naturelle Nationale des Sept-Iles, Pleumeur Bodou, France.

[13] Avian Sleep Group, Max Planck Institute for Ornithology, Seewiesen, Germany.

[14] Núcleo de Teoria e Pesquisa do Comportamento, Universidade Federal do Pará, Belém, Brazil.

[15] Mauritian Wildlife Foundation, Vacoas, Mauritius.

[16] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany.

[17] Department of Biosciences, Swansea University, Swansea, UK.

[*] **Correspondence:** enourani@ab.mpg.de, mahle68@gmail.com, *@elham_nourani*

Summary

Flying seabirds are adapted for windy environments[1,2]. Despite this, storms can cause widespread strandings and wrecks, demonstrating that these seabirds are not always able to avoid or compensate for extreme conditions[3,4,5,6,7]. The maximum wind speeds that birds can operate in should vary with morphology and flight style[8], but this has been hard to quantify due to the challenges of collecting data during infrequent events[9]. Yet this information is crucial for predicting how seabirds are impacted by and respond to extreme events, which are expected to increase in intensity and frequency under climate change[10,11]. We analyzed $>$ 300,000 hours of tracking data from 18 seabird species, representing all major seabird guilds in terms of flight style. We quantified the range of wind speeds that seabirds use during their foraging trips in relation to the wind speeds available, and assessed evidence for avoidance of particular wind conditions. The maximum wind speeds that birds flew in increased with wing loading, in line with general aeronautical predictions. Two species of albatross flew in extreme winds $>$ 23 m s^{-1}. Within the 18 species studied, we found no general preference or avoidance of specific wind speeds. Nonetheless, in a very small number of instances, albatrosses avoided speeds below their operable maxima, demonstrating that even the most wind-adapted birds avoid extreme speeds in particular scenarios. The Atlantic yellow-nosed albatross and the wandering albatross avoided the maximum wind speeds by flying towards and tracking the eye of the storm. Extreme winds therefore might 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.

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

Results

To quantify the wind speeds that seabirds are able to fly in and those they avoid, we analyzed 1,663 foraging trips from 18 species of seabirds, presenting 326,960 hours of flight time. We followed a step-selection approach (Fig. 1), where every two consecutive points along each track (at an hourly scale) were considered as one observed step. Each observed step was matched with a set of 30 alternative steps that shared their start point with the corresponding observed step, but ended in a different location in space within the same time period as the observed step. As such, our dataset had a stratified structure, where 30 alternative steps were matched to one observed step per stratum. We then estimated wind speeds along all observed and alternative steps.

The birds experienced a wide range of wind speeds overall (Fig. 2). However, the variation in wind strength available to them at any one point in time was generally low, with 90% of the strata showing variation lower than 11% (Fig. S1). We found that the wind speeds that the birds used were not significantly different from the strongest speeds available to them (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 (all but the three involving an Atlantic yellow-nosed albatross), 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 albatross and the 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 tested whether morphological characteristics, which largely define flight style, explain species-specific variation in the use of the windscape. Wing loading explained 30-35% of variation in the strength and variation in wind speed (Tables S2 & S3). This result was not influenced by temporal or spatial auto-correlation. Data quantity did not show any correlation with maximum ($r = 0.15$, $p = 0.53$) and variation ($r = 0.33$, $p = 0.17$) of wind speed experienced by different species. We also found no effect of phylogenetic relatedness of the species (Fig. S4) on the distribution of maximum wind speed (*Moran's I* = -0.0006; $p = 0.65$) and wind variability (*Moran's I* = 0.04; $p = 0.43$) that they experienced.

Discussion

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[12], extreme wind conditions have not received the same attention. We show that the maximum flyable wind speeds are predicted by wing loading across different flight styles. This demonstrates the importance of airspeed in wind selectivity, as birds must be able to fly faster than the wind to operate independently of it, and airspeed increases with wing loading. Indeed, the slope of our relationship between wing loading and maximum flyable wind was consistent with the specific prediction that airspeeds vary in proportion to the square root of a bird's wing loading[13]. This highlights two key points, first, that the definition of "extreme" wind speeds varies among species, and second, that aeronautical frameworks for predicting normal operational airspeeds can also provide insight into maximum tolerable wind speeds. It is somewhat surprising that this held across different flight styles, because the maximum airspeeds in flapping fliers are likely limited by the required rates of muscle work[13], whereas the need to maintain force development over the wing within tolerable limits may be critical for dynamic soaring birds[14].

Flight style, which largely determines cost of transport, is also important in determining the upper limits of wind speeds that birds can fly in, as this explained much of the residual variation in maximum flyable wind speed in relation to wing loading. Consequently, while the albatrosses with the highest wing loading flew in the fastest wind speeds (≤ 24 m s^{-1}, 86 km h^{-1}), the Soft-plumaged petrel, which has low body mass (276 g) and wing loading, flew in winds of 20 m s^{-1}. It is likely that dynamic soaring birds differ in the precise strategies they use to operate in (and extract energy from) the strongest winds according to their body size. For instance, smaller birds appear to use greater roll angles which may elicit substantial forces, producing unsustainable torque for the largest albatrosses with their long wings. However, such differences have yet to be investigated.

Quantifying the maximum reference speeds that birds can fly in can provide insight into the conditions that are likely to be costly or risky. This is particularly pertinent for birds at lower latitudes, where fewer tracking data exist[15] and where tropical cyclones form. Our maximum flyable wind speeds for species in higher latitudes are higher than those reported in other bio-logging studies. For instance, in our study, wind speed maxima for albatrosses ranged from 18.9-23.6 m s^{-1}, whereas the previous upper limit reported for Grey-headed (*Thalassarche chrysostoma*), Black-browed (*T. melanophris*) and Wandering albatrosses flying in the Southern Ocean was 20.6 m s^{-1}[16]. Richardson et al. report a maximum wind speed of 18 m s^{-1} for Wandering albatrosses[14]. Catry et al. also describe a Grey-headed albatross flying with a tailwind of 19-22 m s^{-1} in an Antarctic storm[17]. Although, interestingly, Spear and Ainley report observations of small albatrosses flying in 19 and 24 m s^{-1} in normal conditions[18].

Contrary to our expectations, we found almost no evidence that birds avoid the maximum wind speeds that were available to them during the breeding season. Furthermore, the variation in the wind speeds that were available to each species on an hourly basis was low. On the one hand this is intuitive, as birds must breed in areas where they can fly faster than most frequent wind speeds to enable them to return to the nest in almost all conditions, and do so without excessive energetic costs. Nonetheless, while it has been suggested that flight style (which is linked to wind tolerance) represents an important aspect of seabird niche space[19], the role of the windscape in shaping species distributions and diversity has only been investigated for procellariformes[20]. Our data summarizing the wind speeds selected across species therefore provides a starting point for a wider consideration of the role of wind on species with different flight morphologies.

The few instances of avoidance of strong winds in this study may also reflect the fine scale at which we examined wind speed selectivity (using step lengths of one hour). Given that airspeeds typically range from 10 to 18 m s^{-1}[18], 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 behavior as avoidance. Yet adult Great frigatebirds responded to extreme cyclones when the storm eye was 250 km away[21], and Black-naped terns (*Sterna sumatrana*) departed the colony when cyclones were 399 to > 2000 km away[22]. The use of hourly step lengths may therefore 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. This highlights the difficulty of using a single step length to identify responses across species, as birds with lower flight speed may respond to cyclones when they are further away.

Nonetheless, the 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*)[23], 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 therefore be an important part of the behavioral repertoire of fast-flying, wind-adapted species, enabling them to modulate their exposure to unfavorable winds.

Wandering albatrosses also sometimes avoided wind speeds that were well within their normal operational range (14, 15, and 16 m s^{-1}; Fig. S3). 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[1]. Nonetheless, such instances were identified in a minuscule proportion of the movement steps (nine of 93,104).

Overall, our results provide valuable information on the maximum wind speeds that seabirds with variable size and morphology are able to fly in and demonstrate unexpected cases of avoidance in the fastest flying seabirds. Nonetheless, understanding response to global change requires rigorous investigation of outliers and unusual events, and the tools available to the ecological community to study extreme and rare events are limited. We followed a step-selection approach to compare used and available wind speed conditions, but we chose not to proceed with the conditional logistic regressions commonly used to estimate step-selection functions[24], 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 for each step, and thereby identify the rare wind-avoidance events. Yet, in something of a catch-22 situation, our approach was limited by the lack of information about the likely distances over which birds respond to storms. There would likely be benefit in co-opting tools from other fields. For instance, the Extreme Value Theory, commonly used in the field of finance to determine the probability of the occurrence of extreme events[25], could be a promising method to develop a framework uniting susceptibility to extreme weather events with the likelihood that birds will be exposed to them under global change.

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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 and SdG 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.

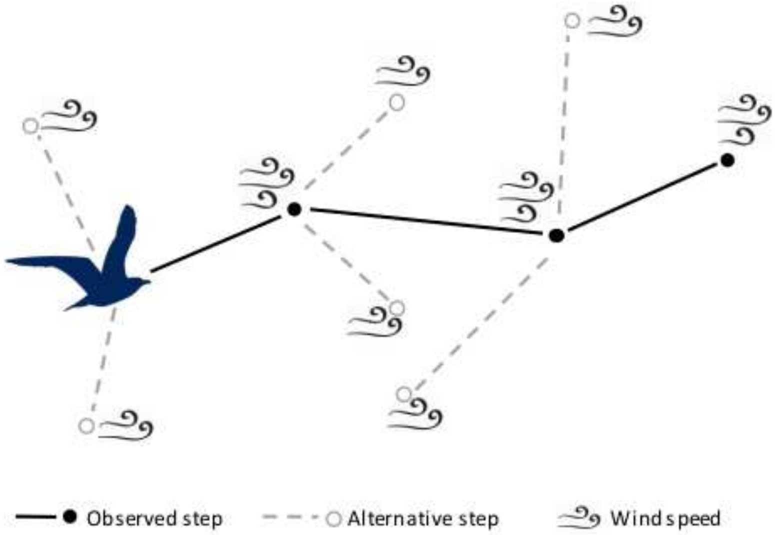

Figure 1: Schematic example of the step-selection approach used in this study. Each pair of consecutive locations is considered as one observed step. Each observed step is associated with a number of alternative steps (2 in this example), creating one stratum. The location of alternative steps is determined 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.

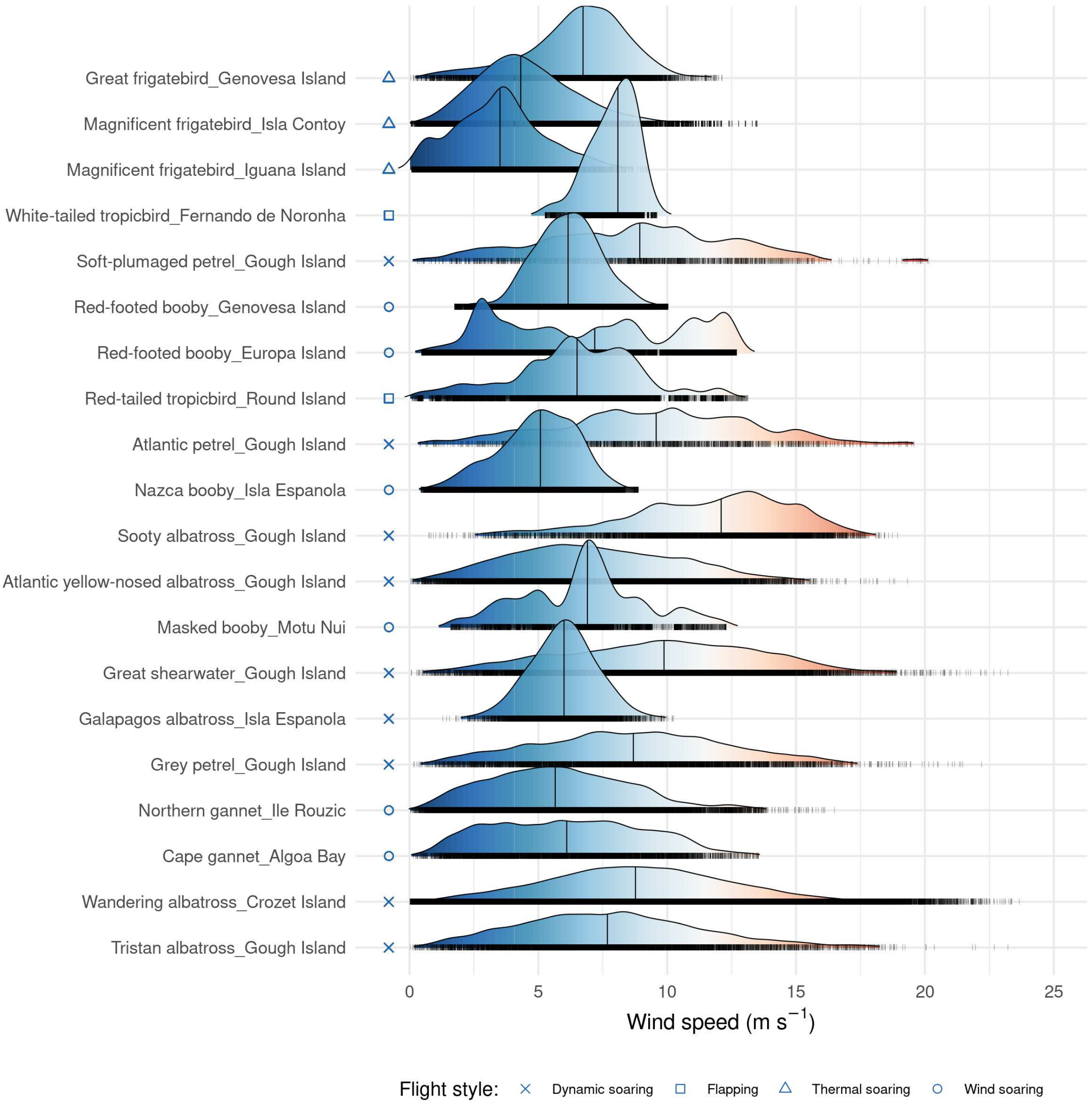

Figure 2: Distribution of wind speeds experienced by each species during foraging trips. Species are ordered by their wing loading (Table S1), with the lowest wing loading at the top. Vertical lines indicate the median.

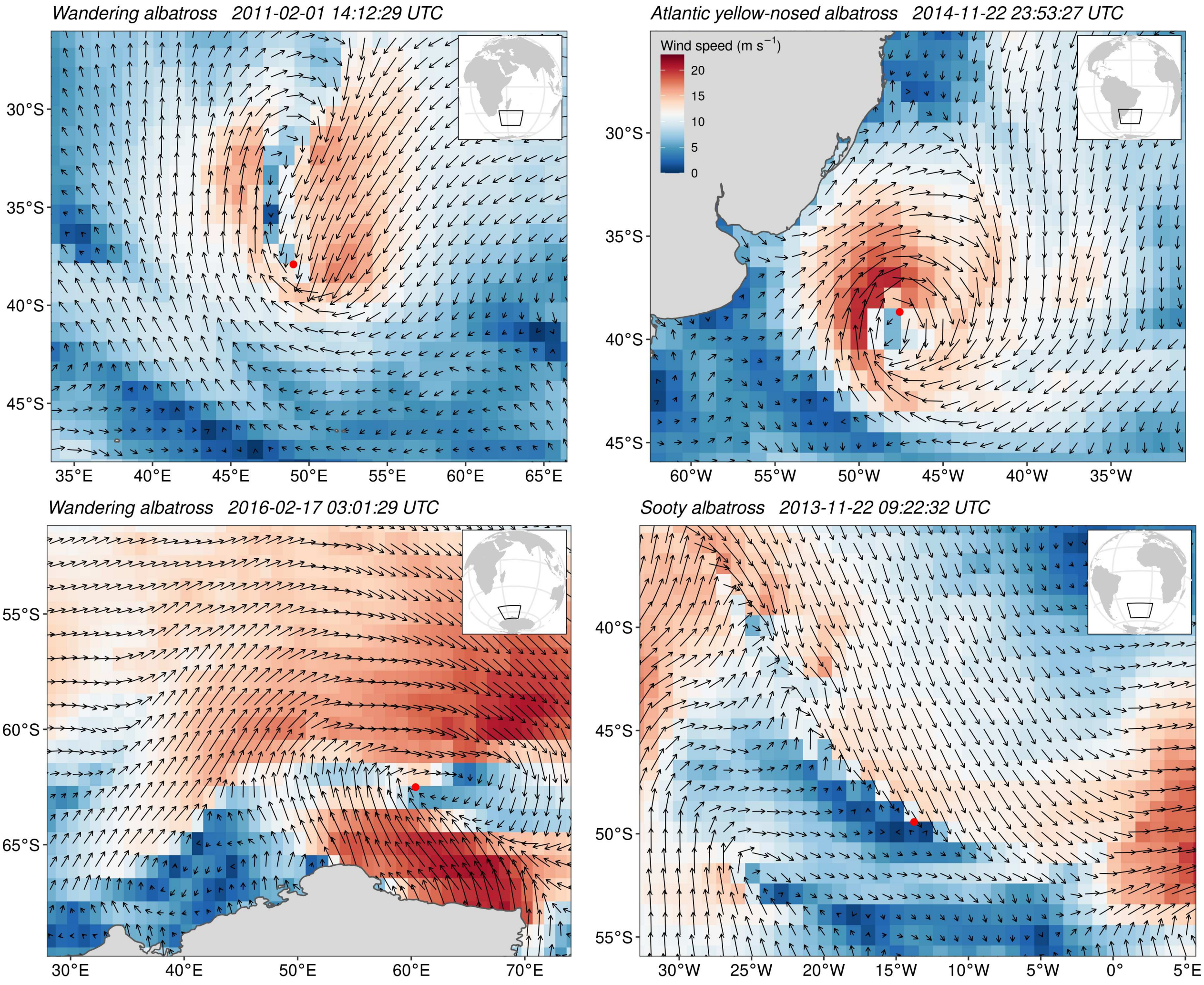

Figure 3: Wind fields at four selected instances where birds (indicated by red dots) avoided the strongest winds. In the top two panels birds appear to avoid the strongest winds associated with cyclonic systems by tracking the low wind region in the eye of the storm. In the bottom two panels birds operated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

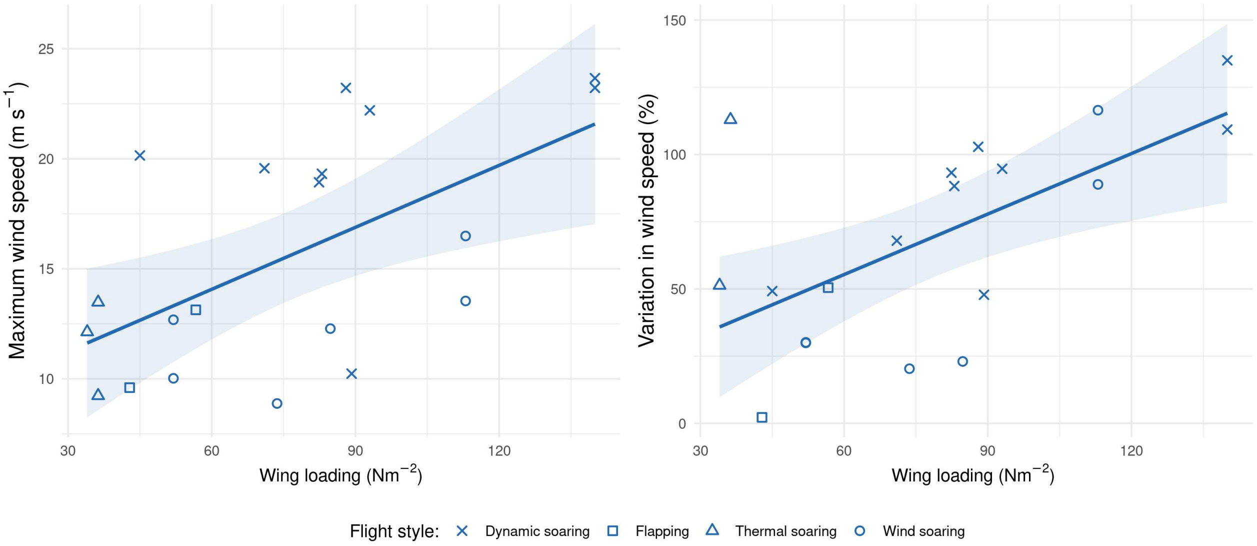

Figure 4: The relationship between wing loading and the maximum strength (left) and variation (right) of wind experienced by the seabirds. Shaded areas show the 95% Confidence Intervals of the regression lines.

Methods

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 of 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 all major seabird guilds in terms of flight style (Table S1), including dynamic soaring (nine species of albatross, petrel, and shearwater), wind soaring (five species of gannet and booby), thermal soaring (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 is scarce for 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[26]). 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 (mode 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.

Data processing

We used a step-selection approach to prepare the data for analysis. This method allowed us to compare the birds' use of the windscape while traveling between foraging sites 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[27] 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. S5).

Previous studies have reported that some species increase their flight height in response to the arrival of cyclones, enabling them to potentially fly above them[21]. Altitude data was available for only three species in our dataset. Inspection of the raw altitude data showed no relationship with wind speed (Pearson correlation test for Red-footed booby: $r = 0.002$, $p = 0.26$; Magnificent frigatebird: $r = -0.043$, $p < 0.05$; Galapagos albatross: $r = -0.050$, $p < 0.05$).

Testing for avoidance of strong wind

We used randomization techniques to test whether seabirds avoided strong winds when foraging at sea. We did not make any assumptions about what wind speeds were considered strong. 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 and variable 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).

We then explored whether variability in wind conditions experienced by each species depended on wing loading. To do this, we calculated the coefficient of variation (CoV) for wind speed values within each stratum. We then modeled the maximum CoV experienced by each population as a function of wing loading. As before, we checked the residuals for spatial and temporal auto-correlation.

The amount of data varied for each species. To test whether the strength and variation in wind speed experienced by different species were affected by the amount of flight data in our dataset, we estimated the correlation between these. We also checked whether phylogenetic distance affected the observed patterns in wind strength and variability by estimating Moran's auto-correlation coefficient[28]. Phylogenetic relationships were extracted from the BirdTree database (*http://birdtree.org*[29]).

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Supplementary Video

Supplementary video: An Atlantic yellow-nosed albatross flies into the eye of the storm. The bird (indicated by a red dot) 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

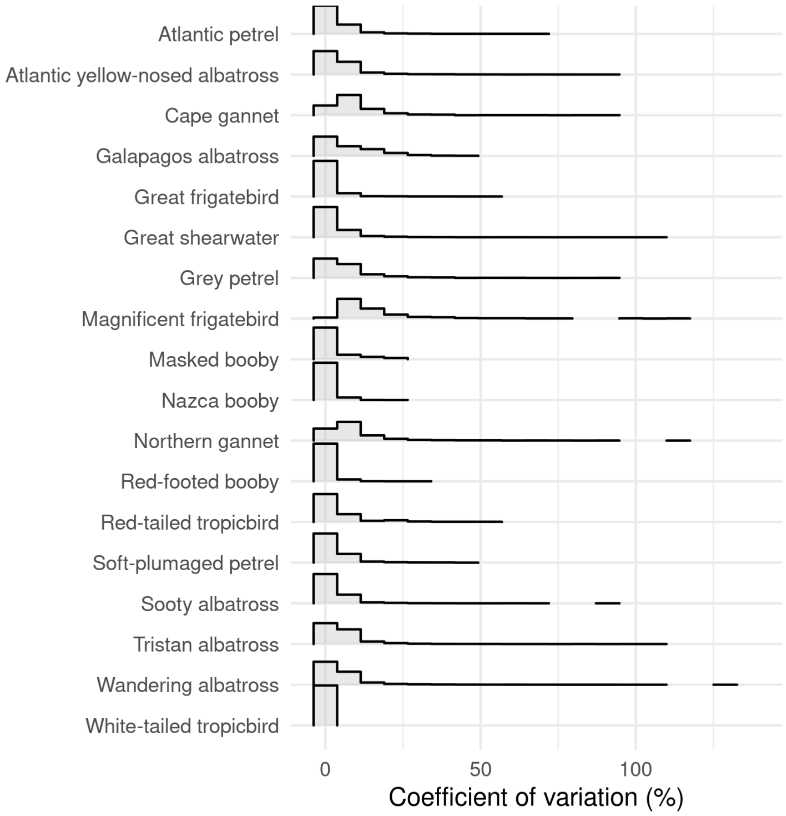

Figure S1: Distribution of coefficient of variation estimated for wind speed within each stratum for each species. Values exceeding 100% indicate higher standard deviation than the mean.

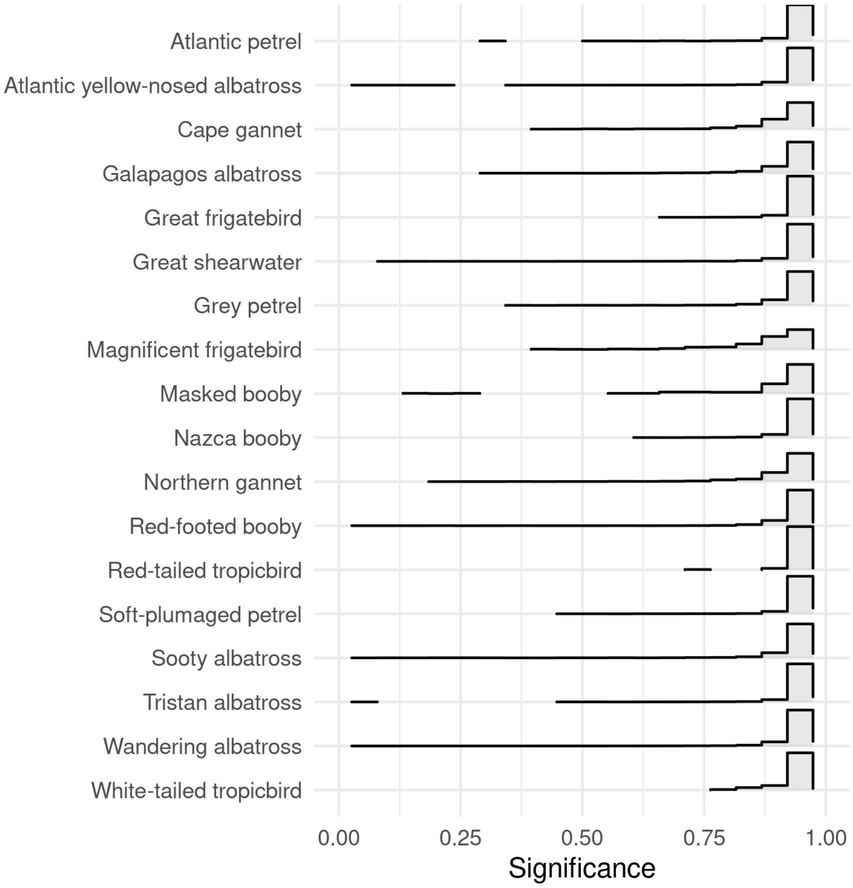

Figure S2: Significance values for randomization tests performed on the stratified dataset to test for avoidance of strong wind. The null hypothesis was accepted in the majority of strata: seabirds did not avoid strong winds. In fact, significant values of 1 indicate that the bird used the maximum wind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

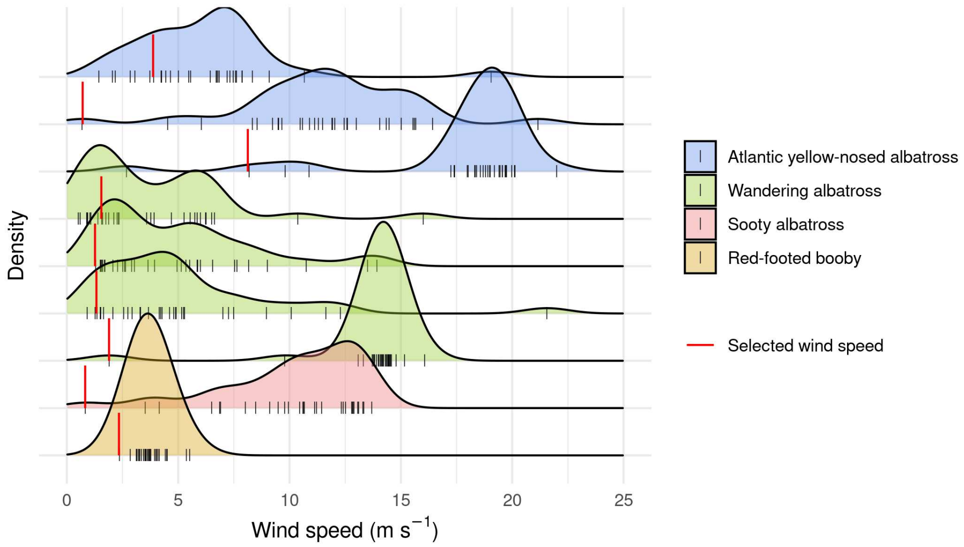

Figure S3: Distribution of available wind speed at the strata where strong wind was avoided.

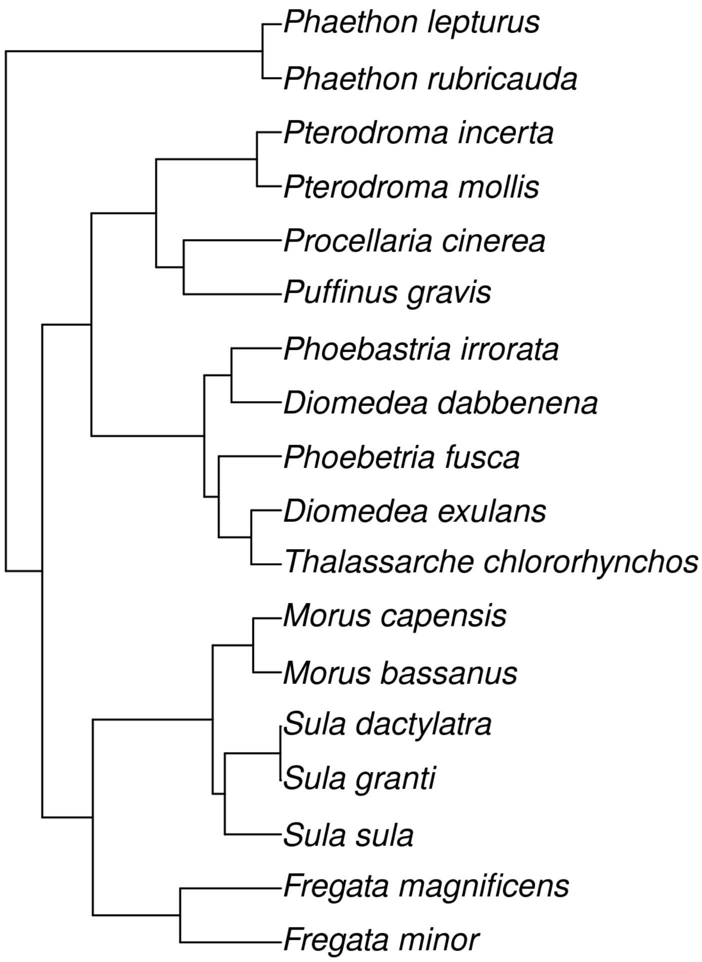

Figure S4: Phylogenetic relationship between the 18 study species, extracted from the BirdTree database (*http://birdtree.org*).

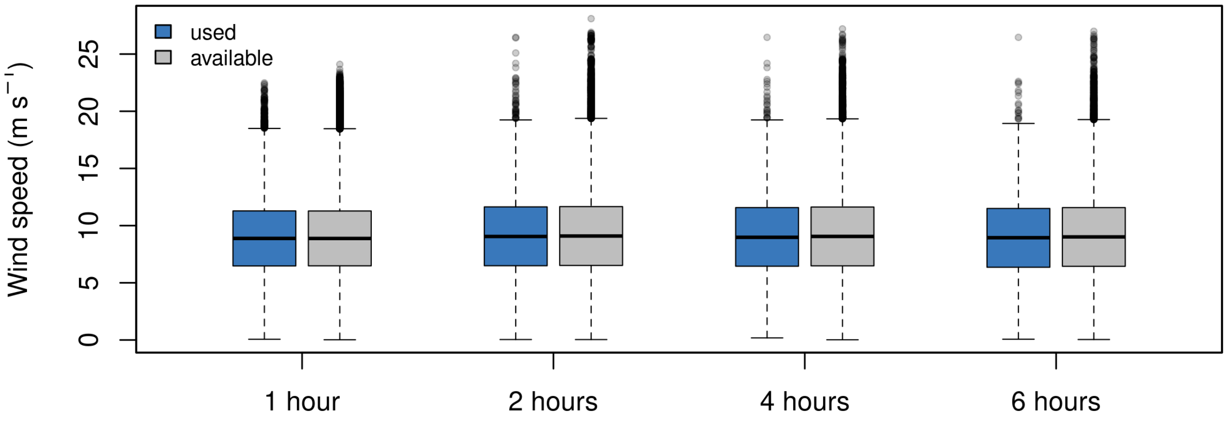

Figure S5: Distribution of wind speed (m s^{-1}) at used and available locations along the wandering albatross foraging tracks for step lengths set to 1, 2, 4, and 6 hours.