

Airflow modelling predicts seabird breeding habitat across islands

Emmanouil Lempidakis¹, Andrew N Ross², Luca Börger¹, and Emily L C Shepard¹

¹Department of Biosciences, Swansea University

²School of Earth and Environment, University of Leeds

January 19, 2021

Abstract

Wind is a fundamental driver of the distribution and energy expenditure of birds at sea. Wind can also influence mortality at the nest. Yet airflows have never been fully integrated into models of breeding habitat selection. We use computational fluid dynamics to provide the first assessment of whether and how airflows predict the distribution of seabird colonies, taking common guillemots (*Uria aalge*) breeding on Skomer island as our study system. We reveal that air pressure predicts occupancy, demonstrating the importance of exposure (rather than wind speed) in habitat selection. Our simple model with pressure and slope correctly identified 80% of the largest colonies and 93% of avoided sites. While previous approaches have not predicted space use in novel sites, our model predicted 73% of the largest colonies on a neighbouring island. This suggests generality in the mechanisms linking airflows and breeding distributions, and highlights a novel route by which seabirds may be affected by global change.

Introduction

For animals operating in aerial and aquatic environments, movement costs and capacities are profoundly affected by air and water currents respectively¹. This drives widespread and large-scale patterns of animal movement; with birds selecting tailwinds or updrafts as they migrate across ocean basins or between land masses², and fish minimising counter-flows as they migrate upstream³. In fish, current selection is also a key driver of habitat use outside periods of travel⁴. Indeed, there is a rich history of research on fish space-use in relation to flow characteristics in rivers dating back to the 1960s⁵, which has demonstrated that water velocity, and in some cases velocity shear, determine abundance, habitat use (both within and between species), and interspecific competition in some species⁴. In contrast, there is little to no research on how local airflows affect the distribution of birds outside travelling, including the distribution of breeding colonies.

Reproductive success is closely linked to the physical characteristics of breeding sites in many taxa^{6,7} which can feed into broader species distribution models⁸. In colonial animals, breeding sites can represent the nexus of reproductive activity for tens of thousands of individuals⁹. There is therefore a clear need to establish what drives colony location in these taxa, in order to identify the availability of breeding habitat, and predict how areas differ in quality, now and in the future¹⁰⁻¹⁶. Over 95% of seabirds are colonial breeders¹⁷. Seabirds are also more at risk than other comparable groups of birds, with widespread decline in populations due to commercial fisheries, pollution, habitat change and the introduction of invasive predators¹⁸. In some cases this has led to entire breeding colonies being lost^{19,20}. Here, conservation practitioners need to know where to focus restoration efforts e.g. by decoy deployment and acoustic attraction to re-seed breeding activity²¹. This is crucial given that there will always be a fitness cost associated with breeding in sub-optimal habitat²². However, while a wide range of studies have analysed breeding site characteristics in seabirds^{6,7,9,23}, and compared them with available habitat²⁴, we are unaware of any that have successfully applied predictions from one site to another (*cf.* ²⁵).

The tendency of seabirds to breed on offshore islands and/ or coastal cliffs has been attributed to the need to reduce exposure to terrestrial predators and be close to feeding areas^{9,26}. Nonetheless, for cliff nesting species, it is clear that not all cliffs are equal, as colonies tend to be clumped, with great swathes of cliff habitat left empty⁷. Indeed, cliffs should vary in their accessibility to terrestrial predators (primarily through variation in slope angle), as well as the availability of suitable breeding ledges, with species varying in their need for different ledge characteristics according to their body size and nest building habit^{6,27}.

There are also compelling reasons why flow characteristics should affect breeding habitat preferences, particularly for groups such as seabirds, which are exposed to strong flows. Wind can affect the risk of eggs/ birds being displaced from the nest²⁸, as well as influencing exposure to rain (particularly in cliff nesting species) and heat stress (through evaporative heat loss), both of which can cause mortality^{28,29,30}. Wind also has a strong influence on flight capacity. In common guillemots (*Uria aalge*) and razorbills (*Alca torda*), 60% of attempts to land at their cliff nests were found to fail in a strong breeze³¹, suggesting there are advantages to breeding on more sheltered cliffs. Indeed, frigatebirds (*Fregata magnificens*) nest in relatively wind still areas, despite the associated reduction in ability of birds to lose heat, which may reflect the difficulties that adults would experience in remaining on the nest and operating close to it in high winds due to their low weight and wing loading³². The importance of being able to maintain flight control close to the nest suggests that habitat selection could be influenced by several airflow characteristics, including the strength of the horizontal and vertical components, as well as the turbulence.

Despite the potential importance of airflows for these animals that breed in exposed locations, there is a complete lack of information on the flow characteristics associated with colony presence and absence (though see³³). This is likely due to the difficulties of quantifying wind over complex, often steep terrain. It may also reflect our inability to see flow characteristics, in contrast to rivers where this can be evident from surface characteristics. Where the impact of wind has been assessed by proxy, wind fetch was found to have contrasting effects in the presence/absence of colonies of three *Pygoscelis* penguin species³⁴, while colony aspect was not significant for species of the auks family^{23,31}. Nonetheless, aspect may be a poor proxy for the precise wind conditions experienced at colonies, as airflow characteristics will be modified by the particular topography of the surrounding area. As a result, two cliffs with the same aspect and prevailing wind conditions can experience very different flow regimes³¹.

We use computational fluid dynamics (CFD) to provide the first assessment of whether and how local airflow conditions predicts the distribution of seabirds, taking colonies of common guillemots (*Uria aalge*) breeding on Skomer island, UK, as our study system. We estimate a number of airflow characteristics, including the magnitude of the wind, the horizontal and vertical wind components, air pressure (as a predictor of exposure) and finally gustiness and turbulence, which may affect flight control close to the breeding cliffs³¹. Our specific objectives were to: (i) assess whether airflows associated with the prevailing wind direction predict breeding site selection (patterns of presence and absence), and habitat quality (colony density), (ii) quantify the airflow conditions that birds will be exposed to with changes in wind direction and (iii) test our model of habitat selection by predicting colony presence and absence on a neighbouring island. This test that is considerably stronger than standard cross-validation, but rarely performed²⁵. Overall, our approach should provide insight into the conditions birds select and avoid in the prevailing wind, and the “penalty” they suffer in terms of the adverse conditions they are exposed to if the wind direction changes, either over the short-term, or as part of larger scale climatic shifts^{35,36}.

Results

Prevailing environmental conditions

Winds around Skomer are predominantly from the SW, although there is some variation with wind strength, as light winds ($< 6 \text{ m s}^{-1}$) are equally likely to be from the SW or NW (Supplementary Fig. 2a,b). Overall, easterly winds are the least frequent (Supplementary Table 1).

Environmental parameters associated with colony distribution on Skomer island

Wilcoxon rank sum tests for all colony classifications revealed statistically different slope angles between colonies and non-colonies on Skomer Island (taking any positive count of birds as colony presence, $W = 611724994$, $p\text{-value} < 2.2e-16$). Unoccupied sections were generally less steep than occupied sections (median slope angles 45° and 51° respectively) and the densest and largest colonies were associated with the steepest cliffs (Fig. 1). Slope angle varied with cliff orientation, with mean slope angle being lowest for cliffs with S and SE orientations. Interestingly, cliffs facing SW have relatively high mean slope angles (Fig. 1a). Despite this, most occupied sections were orientated away from the SW (Fig. 2a). Both the largest, as well as the densest colonies, were mainly orientated towards the NW and E.

Models of wind and slope angle significantly predicted colony presence and absence on Skomer, with the model correctly identifying 80% of the colonies and 93% of avoided sites for a SW wind, where presence was taken as the 10 largest colonies (Table 1). In fact, models of colony location performed well across all modelled wind directions except for SE winds, indicating that colonies are characterised by particular sets of flow characteristics in most scenarios. Indeed, in each wind direction, one colony classification could be predicted by airflow parameters alone, without slope angle. The lowest model performance was seen with SE winds where only one colony classification yielded a reasonable model fit (McFadden⁴¹ $R^2[?]$ 0.2, table 1). In this model, colony presence was predicted by slope angle alone (Table 1).

Across the different colony classifications, the pseudo R^2 was lowest overall in models of any occupancy (1st classification SW 0.28; NW 0.24, SE 0.12, NE 0.38) compared to those predicting the 10 largest colonies (2nd classification SW 0.59; NW 0.58, SE 0.32, NE 0.74) or the 11 densest (3rd classification SW 0.17; NW 0.40, SE 0.15, NE 0.67) (Table 1). The overall accuracy and true skill statistics followed the same general trend, being highest for the 10 largest colonies (Table 1). The sensitivity tended to be somewhat lower than specificity in the 1st classification (sensitivity was: SW 0.63; NW 1.00, SE 0.21, NE 0.60 and specificity was: SW 0.69; NW 0.21, SE 0.96, NE 0.84), but increased in the 2nd and 3rd classifications indicating a better ability to predict true presence compared to true absence for the largest and densest colonies.

While mean slope angle was included in two of three models for SW, NW and NE wind directions, airflow parameters always had a higher effect size (SI Table 2). A narrow set of airflow parameters was identified as significant in predicting colony presence across wind directions (Table 1). Furthermore, there was broad agreement between the airflow characteristics identified within each wind direction, irrespective of the way colonies were classified. Pressure statistics were included in all SW models, while TKE and horizontal wind speed parameters were included in all NW and NE models, respectively.

Unexpectedly, wind speed (in terms of median or skewness) was not included in the simplest top models of SW winds, instead colonies were associated with a lower median pressure and pressure gradient (Table 1), both of which are linked to lower exposure (Fig. 2, Fig. 3).

Colonies were associated with higher turbulence compared to unoccupied sites, particularly in the case of NW and NE winds (Table 1). In NE winds, colonies experienced both higher wind speeds (Fig. 4) (positive horizontal median, 1st classification and negative horizontal skewness, 2nd and 3rd classifications) and higher turbulence (here TKE estimates in the 1st and 3rd classifications).

Predicting colony distribution on Skokholm

The model predicting the largest colonies on Skomer under SW winds also performed well when applied to the island of Skokholm (Fig. 5), correctly predicting the distribution of $\sim 73\%$ of the largest colonies (eight out of eleven), and $\sim 63\%$ of unoccupied cliff sections (35 out of 56), which corresponds to $\sim 80\%$ of the total unoccupied area ($60,863 \text{ m}^2$ of $76,259 \text{ m}^2$). Model performance, although lower than the models on Skomer, was satisfactory with an overall accuracy of 0.64 and TSS 0.35.

Discussion

Wind regimes are changing, in terms of the mean strength, and the frequency of extreme weather events^{35,36}. Yet research on how wind affects seabirds has focused on their at-sea behaviour (though see^{37,34}). Through our novel application of CFD, we demonstrate that airflows are also critical in the selection of breeding

habitat. Areas of coastline vary predictably in their exposure to prevailing wind conditions, and we show this is an important driver of habitat preference in cliff-nesting auks. Interestingly, while colony location was predicted by low exposure to the prevailing wind, it was not predicted by low wind speed. This apparent contradiction is explained by the fact that windward cliffs can block the oncoming flow, with the blocking effect increasing with cliff height and slope, producing low wind speeds and high pressures over large parts of windward cliffs (bar the top, where flow is accelerated, Fig 3a,b). Areas of low wind speed therefore occur on both windward and leeward cliffs (Supplementary Fig. 3), but guillemots select the latter. This suggests habitat selection is driven as much by the need to shelter young from the impact of rain or wave action (both of which should increase with exposure), as it is to shelter from high wind speeds, which can affect wind chill³⁸ and flight capacity (either of the guillemots or their aerial predators^{31,38}). Nonetheless, flight capacity may be more critical for species such as large albatrosses, which require relatively high winds to take-off and therefore may be constrained to nest in exposed areas, despite the intuitive benefits of shelter for chicks across species.

Our models confirm the role of slope angle in colony selection, with the densest and largest colonies on Skomer being associated with the steepest cliffs. Steep slopes offer the possibility of breeding in high densities with better protection from predators³⁹, as well as easier access to the sea when chicks jump from their nests^{40,41}. Yet here we show that steep cliffs with a south-westerly orientation are avoided on Skomer, even though they are widely available. This trend was not significant in a previous assessment of whether colonies varied in aspect³¹, confirming our prediction that cliff aspect alone is not a good proxy for exposure. Furthermore, the fact that slope angle had a lower contribution in our models than pressure and turbulence, suggests that colonies are better tuned to wind rather than topographical features.

While guillemots preferentially breed in areas that are not exposed to the prevailing wind, they cannot shelter from all wind directions. Winds diametrically opposed to the prevailing direction (here NE winds) will be problematic for any species breeding in sheltered sites. The penalty of exposure to NE winds for the 10 largest colonies on Skomer, was a ~10% increase in mean wind speed compared to the same at-sea wind speeds from the SW. How this might impact birds will depend on the factors driving the need for shelter and the magnitude of the wind when it comes from a different direction. Nonetheless, our results highlight that colonies experience increased exposure from changes in wind direction, independent of rising wind speeds. Increases in wind speed, as already observed in the North Atlantic and other areas^{35,36}, are also likely to be most detrimental to birds at the nest when accompanied by a change in wind direction³⁷.

A further challenge potentially facing birds on Skomer in NE and NW winds is increased turbulence. The absolute levels of turbulence that birds experience in SW winds are low because the wind speeds themselves are low. However, in NE winds of the same magnitude, birds experience both stronger winds and increased turbulence. Wind speed has been shown to reduce the probability of guillemots landing successfully at their breeding cliffs³¹ and turbulence is likely to present further difficulties for flight control in stronger winds^{42,43}.

The fact that our models performed better in correctly predicting the densest colonies, compared to the presence of any breeding birds, suggests that they work best in predicting high quality habitat. Previous studies have shown that breeding success increases with the density of breeding pairs^{7,44}. Appropriate areas that can support larger numbers are therefore of higher quality. Such areas have previously been described in terms of the number of walls, slope and width of the ledge where the egg was incubated, and distance from the top of the cliff^{6,7}. The ability to predict high quality breeding habitat without such fine-scale topographical information is advantageous, as it allows habitat quality to be predicted in remote and inaccessible sites.

Models of absence should be interpreted with more caution than models of presence, as cliffs that are unoccupied now may have been occupied in the past. Indeed, photographs of the breeding cliffs on Skomer from the 1930s provide evidence that numbers were much higher historically⁴⁵, and whole island counts undertaken since 1963 demonstrate that numbers have been increasing since then⁴⁶. The relative abundance of common guillemots makes this less of an issue than for many species where current breeding activity occurs in a small fraction of the former range. In cases where populations are increasing, our approach could be extended to see whether airflow characteristics can predict colony growth rates, or which areas most likely

to be expanded into.

Overall, the fact that 90% of the densest colonies on Skomer could be predicted solely from variation in pressure values i.e. without the need for slope angle, is testament to the predictive power of our approach. CFD is particularly well-suited to modelling habitat selection in seabirds, as marine and coastal environments experience some of the most extreme wind conditions⁴⁷, and wind fields also tend to be reasonably laminar ahead of islands. A key future challenge will be to test this approach over larger areas. Combining airflow modelling with data on rainfall and breeding success will also provide new mechanistic insight into the basis for habitat selection and how global change may impact birds at their nesting sites.

Methods

Our approach centres around the estimation of airflow parameters around Skomer Island (51° 44.271'N, 5° 17.668'W) and the use of these parameters, in combination with slope angle, from a highly resolved LiDAR digital elevation model, to predict the distribution of breeding guillemots on Skomer and then on the neighbouring island of Skokholm. The 2015 Skomer guillemot breeding bird survey⁴⁸ was digitized in ArcMap 10.5.1 (ESRI, Redlands, California) and used to delineate sections on the island's cliffs that were occupied by breeding birds. It was also used to identify the 10 largest colonies (count [?] 592 individuals) and 11 densest colonies (density [?] 0.835, birds per sq. m), with thresholds being selected by visually identifying clear breakpoints.

A “digital elevation model” (DEM) (50 cm resolution retrieved from Lle Geo-Portal <http://lle.gov.wales>) was used to identify cliff habitat by selecting slopes [?] 20° (initial trials showed this value performed well in isolating cliff habitat). The resultant area was divided into sections according to those used in the breeding survey. These same sections (71 in total) were used in all further analyses, 38 of which were occupied by breeding birds (Fig. 2 a). The minimum height of each section was taken as 10 m to account for variation in tide height (maximum tide height ~ 5 m on the day the DEM was produced), the maximum wave height (taken to be 3 m), as well as a minimum distance above water that birds tend to nest, taken to be 2 metres⁷. The maximum height of each section was reduced using a minimum distance of 15 m from the top of the cliff. This distance was the mean proximity of nests from the top of the cliffs for three major colonies, based on highly resolved theodolite measurements⁴⁹.

A similar approach was taken to digitize the distribution of breeding guillemots on Skokholm from the 2018 breeding bird survey⁵⁰ (Supplementary Fig. 1a). However, because the elevation of Skokholm's cliffs is much lower, the minimum distance from the top of the cliffs, was set at 7 m (this value was arrived at in consultation with the wardens). The small proportion of occupied cliffs that did not satisfy this threshold were not mapped. In the cases where estimates of bird numbers were given in relation to a single point on the map, we used a minimum section length of 30 m of coastline, unless ascribing this width to adjacent colonies would have resulted in unoccupied sections of < 30 m, in which case we assigned a section of 30-50 m in length. This approach resulted in 35 colonised areas from a total of 91 (Supplementary Fig. 1b).

Computational fluid dynamics modelling of wind conditions

In order to assess whether breeding distributions are affected by airflow characteristics, wind conditions around the cliffs of Skomer were simulated using the computational fluid dynamics (CFD) model OpenFoam (openfoam.org version 5.x). OpenFoam is widely used for modelling atmospheric boundary layer flows (e.g. in the wind energy industry) and has been extensively validated over a similarly steep island⁵¹.

The initial coarse model domain was 5300 x 5000 x 1000 m, with a horizontal resolution of 20 m and a vertical resolution of 10 m. The bottom boundary represented the surface of the island which was taken from a DEM of Skomer with 2 m resolution (Lle Geo-Portal <http://lle.gov.wales>). A simulation was also run using the DEM with 1 m resolution, however, the outputs were not significantly different. After establishing the initial mesh, the tool snappyHexMesh in OpenFoam was used to incorporate the DEM into the modelling process, refining initial mesh cells close to the surface up to 3 times. This resulted in a finer resolution close to surface of 2.5 m in the horizontal and 1.25 m in the vertical. Simulations were completed when convergence was

achieved using a steady-state incompressible solver with a $k-\epsilon$ turbulence closure scheme.

Wind simulations were run for NW, NE, SE and SW wind directions to cover a representative sample of wind directions, including the prevailing SW direction (see Results). This allowed us to test whether birds selected sites that were predicted by a specific set of wind parameters across wind directions. The initial wind speed was set to 10 m s^{-1} at 20 m height. The following airflow characteristics were extracted from the model output at 2 m normal to the ground surface (this height was selected in order to estimate the airflow conditions that birds would be exposed to close to their breeding cliffs): The two horizontal and vertical wind vectors (U_0, U_1 and U_2 respectively), mean wind speed (MeanU), turbulent kinetic energy (TKE), pressure (P), kinematic viscosity (Nut) of the air medium and turbulence dissipation rate (ϵ). These outputs were further used to estimate horizontal wind speed; gustiness and turbulence intensity (TI) following³¹.

Statistical analysis

Each of the four OpenFoam simulations (i.e. for NW, NE, SE and SW wind directions) resulted in 76,913 data points across all cliff sections. For each wind direction, the modelled airflow parameters within each occupied/ unoccupied section were reduced to the following summary statistics; median, interquartile range (IQR) and skewness. Median statistics were used to identify the strength of each wind parameter within a section. The IQR values identify the variability or gradient of each wind parameter within a section. High skewness statistics for horizontal wind speed (skewed right) correspond to shelter.

The complete set of 27 airflow parameters was tested for collinearity by producing a correlation hierarchy table for each initial wind condition. Highly correlated terms (Pearson correlation coefficient [?] 0.7) were removed from the analysis, leading to the inclusion of 15 wind parameters. The mean slope steepness per section was added to the total set and parameters were standardized using the MuMin package⁵² version 1.43.17.

We considered that it would be stretching the data to model the density or number of breeding birds as a continuous variable, particularly as the extent of each section was determined by the need to survey cliffs, and did not accord with the beginning or end of occupied/ unoccupied areas. We therefore ran separate models, with colony presence defined as (i) the presence of any breeding birds, (ii) the largest (iii) the densest colonies. For the latter two categories, areas with breeding birds that did not fall into either the largest or densest categories were excluded from the modelling process instead of defining them as absence. The excluded areas represented 23.5% and 27.7% of all breeding birds respectively. This resulted in trained datasets of 43 and 44 sections for the largest and densest datasets.

A two-step approach was used to build the global model and identify the final, best-fitting models. First, to reduce the large number of covariates, a random forest classifier was fitted, using the package randomForest⁵³ version 4.6.14. The 10 most important terms were selected to build the global logistic regression model. This parameter set was further simplified using the dredge function (MuMin package⁵²), to perform stepwise Bayesian information criterion (BIC) selection, penalising for model size. In the case of the models for largest and densest colonies in a NW wind, the number of terms in dredge had to be gradually reduced to eight and seven respectively, to prevent fitting of models with probabilities of zero and one. The simplest model among those with a difference in BIC [?] 2 was selected as the best final model.

The final model was assessed for goodness of fit using the McFadden⁵⁴ pseudo R^2 . Values between 0.2 – 0.4 were considered as very satisfactory⁴². Model performance was also evaluated in terms of overall accuracy (OA); true skill statistic (TSS), sensitivity and specificity^{55,56}. The effect size of each predictor included in the final model was determined by computing the odds ratio.

The previous steps were repeated for all four initial wind directions, with three logistic regression models of colony presence/absence implemented per direction, in order to identify links between wind and slope that were robust to different classifications of breeding colony. All statistical analyses were conducted in R⁵⁷ version 3.6.3 and RStudio⁵⁸ version 1.1.463.

Acknowledgements

We are grateful to the Wildlife Trust of South and West Wales, Skomer wardens Bee Büche and Eddie Stubbings, and Skokholm wardens Giselle Eagle and Richard Brown, for providing the survey maps used in this study, and to Dr Ben Evans for discussions on interpreting pressure fields. We thank Natural Resources Wales for providing the wind data from the Coastguard lookout station at Wooltack point. EL and ELCS are supported by the European Research Council under the European Union's Horizon 2020 research and innovation program Grant 715874 (to ELCS).

Competing Interests

The authors declare no competing interests.

Manuscript format: Nature

Authorship statement: The study was conceived by ELCS and AR. EL undertook the data analysis with input from all authors. The manuscript was first drafted by EL and ELCS with further contributions from all authors.

Data statement: All data generated or analysed during this study are included in the submission of this article (and its supplementary information files) and will be available with publication.

References

- 1 Shepard, E. L. *et al.* Energy landscapes shape animal movement ecology. *The American Naturalist* **182** , 298-312 (2013).
- 2 Flack, A., Nagy, M., Fiedler, W., Couzin, I. D. & Wikelski, M. From local collective behavior to global migratory patterns in white storks. *Science* **360** , 911-914 (2018).
- 3 Smith, R. J. F. *The control of fish migration* . Vol. 17 (Springer Science & Business Media, 2012).
- 4 Heggenes, J. Habitat utilization and preferences in juvenile Atlantic salmon (*Salmo salar*) in streams. *Regulated Rivers: Research & Management* **5** , 341-354 (1990).
- 5 Elson, P. Effects on wild young salmon of spraying DDT over New Brunswick forests. *Journal of the Fisheries Board of Canada* **24** , 731-767 (1967).
- 6 Birkhead, T., Greene, E., Biggins, J. & Nettleship, D. Breeding site characteristics and breeding success in Thick-billed Murres. *Canadian Journal of Zoology* **63** , 1880-1884 (1985).
- 7 Harris, M., Wanless, S., Barton, T. & Elston, D. Nest site characteristics, duration of use and breeding success in the Guillemot *Uria aalge*. *Ibis* **139** , 468-476 (1997).
- 8 Fielding, A. H. & Haworth, P. F. Testing the generality of bird-habitat models. *Conservation biology* **9** , 1466-1481 (1995).
- 9 Buckley, F. G. & Buckley, P. A. in *Behavior of marine animals* 69-112 (Springer, 1980).
- 10 Frid, A. & Dill, L. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6** (2002).
- 11 Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421** , 37-42 (2003).
- 12 Jetz, W., Wilcove, D. S. & Dobson, A. P. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol* **5** , e157 (2007).
- 13 Sorte, F. A. L. & III, F. R. T. Poleward shifts in winter ranges of North American birds. *Ecology* **88** , 1803-1812 (2007).
- 14 Dunlop, J. The population dynamics of tropical seabirds establishing frontier colonies on islands off south-western Australia. *Marine Ornithology* **37** , 99-105 (2009).

- 15 Chambers, L. E. *et al.* Observed and predicted effects of climate on Australian seabirds. *Emu-Austral Ornithology* **111** , 235-251 (2011).
- 16 Rushing, C. S., Royle, J. A., Ziolkowski, D. J. & Pardieck, K. L. Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change. *Proceedings of the National Academy of Sciences* **117** , 12897-12903 (2020).
- 17 Rolland, C., Danchin, E. & Fraipont, M. d. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *The American Naturalist* **151** , 514-529 (1998).
- 18 Croxall, J. P. *et al.* Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International* **22** , 1-34 (2012).
- 19 Jones, H. P. *et al.* Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology* **22** , 16-26 (2008).
- 20 Brooke, M. d. L. *et al.* Seabird population changes following mammal eradications on islands. *Animal Conservation* **21** , 3-12 (2018).
- 21 Jones, H. P. & Kress, S. W. A review of the world's active seabird restoration projects. *The Journal of Wildlife Management* **76** , 2-9 (2012).
- 22 Brown, J. L. Territorial behavior and population regulation in birds: a review and re-evaluation. *The Wilson Bulletin* , 293-329 (1969).
- 23 Keslinka, L. K., Wojczulanis-Jakubas, K., Jakubas, D. & Neubauer, G. Determinants of the little auk (Alle alle) breeding colony location and size in W and NW coast of Spitsbergen. *PloS one* **14** , e0212668 (2019).
- 24 Clark, L., Ricklefs, R. E. & Schreiber, R. Nest-site selection by the Red-tailed Tropicbird. *The Auk* **100** , 953-959 (1983).
- 25 Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31** , 140-160 (2008).
- 26 Cody, M. Ecological Adaptations for Breeding in Birds. Davi Lack. Methuen, London, 1968 (U. S. distributor, Barnes and Noble, New York). xii + 409 pp., illus. \$15. *Science* **163** , 1185-1187, doi:10.1126/science.163.3872.1185 (1969).
- 27 Squibb, R. C. & Hunt Jr, G. L. A Comparison of Nesting-Ledges Used by Seabirds on St. George Island. *Ecology* **64** , 727-734 (1983).
- 28 Hamer, K. C., Schreiber, E. & Burger, J. Breeding biology, life histories, and life history-environment interactions in seabirds. *Biology of marine birds* , 217-261 (2001).
- 29 Dunn, E. The role of environmental factors in the growth of tern chicks. *The Journal of Animal Ecology* , 743-754 (1975).
- 30 Konarzewski, M. & Taylor, J. R. The influence of weather conditions on growth of little auk Alle alle chicks. *Ornis Scandinavica* , 112-116 (1989).
- 31 Shepard, E., Cole, E.-L., Neate, A., Lempidakis, E. & Ross, A. Wind prevents cliff-breeding birds from accessing nests through loss of flight control. *eLife* **8** , e43842 (2019).
- 32 Diamond, A. W. S. E. A. in *The Birds of North America* (ed A. F. Poole and F. B. Gill) (Cornell Lab of Ornithology, 2002).
- 33 Burger, J. & Lesser, F. Selection of colony sites and nest sites by common terns *Sterna Hirundo* in ocean county, New Jersey. *Ibis* **120** , 433-449 (1978).

- 34 Schrimpf, M. & Lynch, H. The role of wind fetch in structuring Antarctic seabird breeding occupancy. *Ibis* .
- 35 Young, I., Zieger, S. & Babanin, A. V. Global trends in wind speed and wave height. *Science* **332** , 451-455 (2011).
- 36 Young, I. R. & Ribal, A. Multiplatform evaluation of global trends in wind speed and wave height. *Science* **364** , 548-552 (2019).
- 37 Weimerskirch, H., Louzao, M., de Grissac, S. & Delord, K. Changes in wind pattern alter albatross distribution and life-history traits. *science* **335** , 211-214 (2012).
- 38 Kulaszewicz, I. & Jakubas, D. Influence of nest burrow microclimate on chick growth in a colonial High-Arctic seabird, the little auk. *Polar Research* **37** , 1547044 (2018).
- 39 Birkhead, T. R., Thompson, J. E. & Montgomerie, R. The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces. *The Auk: Ornithological Advances* **135** , 1020-1032 (2018).
- 40 Berger, U. Tissue distribution of perfluorinated surfactants in common guillemot (*Uria aalge*) from the Baltic Sea. *Environmental science & technology* **42** , 5879-5884 (2008).
- 41 Gilchrist, H. G. & Gaston, A. J. Factors affecting the success of colony departure by thick-billed murre chicks. *The Condor* **99** , 345-352 (1997).
- 42 Combes, S. A. & Dudley, R. Turbulence-driven instabilities limit insect flight performance. *Proceedings of the National Academy of Sciences* **106** , 9105-9108 (2009).
- 43 Ortega-Jimenez, V. M., Sapir, N., Wolf, M., Variano, E. A. & Dudley, R. Into turbulent air: size-dependent effects of von Karman vortex streets on hummingbird flight kinematics and energetics. *Proceedings of the Royal Society B: Biological Sciences* **281** , 20140180 (2014).
- 44 Birkhead, T. R. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *The Journal of Animal Ecology* , 751-764 (1977).
- 45 Harris, M. P. Population changes in British common murres and Atlantic puffins, 1969-88. (1991).
- 46 Meade, J., Hatchwell, B. J., Blanchard, J. L. & Birkhead, T. R. The population increase of common guillemots *Uria aalge* on Skomer Island is explained by intrinsic demographic properties. *Journal of avian biology* **44** , 055-061 (2013).
- 47 Wiley, J. W. & Wunderle, J. M. The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Conservation International* **3** , 319-349 (1993).
- 48 Stubbings, E., Buche, B., Riera, E. M., Green, R. & Wood, M. J. Seabird monitoring on Skomer Island in 2015. *Seabird monitoring on Skomer Island in 2015* (2015).
- 49 Cole, E.-L. *et al.* The Ornithodolite as a tool to quantify animal space use and habitat selection: a case study with birds diving in tidal waters. *Integrative zoology* **14** , 4-16 (2019).
- 50 Brown, R. & Eagle, G. Skokholm Seabird Report 2018. (2018).
- 51 Bechmann, A., Sorensen, N. N., Berg, J., Mann, J. & Rethore, P.-E. The Bolund experiment, part II: blind comparison of microscale flow models. *Boundary-Layer Meteorology* **141** , 245 (2011).
- 52 Barton, K. & Barton, M. K. Package ‘MuMIn’. *Version* **1** , 18 (2015).
- 53 Liaw, A. & Wiener, M. Classification and regression by randomForest. *R news* **2** , 18-22 (2002).
- 54 McFadden, D. Conditional logit analysis of qualitative choice behavior. (1973).
- 55 Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology* **43** , 1223-1232 (2006).

56 Borger, L. & Nudds, T. D. Fire, humans, and climate: modeling distribution dynamics of boreal forest waterbirds. *Ecological Applications* **24** , 121-141 (2014).

57 Team, R. C. R: A language and environment for statistical computing. (2020).

58 RStudio: Integrated Development Environment for R (Boston, MA, 2015).

Figure 1. Slope angles selected by breeding birds in relation to those available on Skomer. a) Mean slope angle ($^{\circ}$) according to orientation (number of points per orientation bin; 2911- 8718). b) Slope angle in relation to (A) unoccupied sections ($n=33$, median= $\sim 45.1^{\circ}$), (B) occupied but not classified as either largest or densest sections ($n=31$, median= $\sim 47.5^{\circ}$) and (C) sections classified as both largest and densest ($n=7$, median= 68.5°).

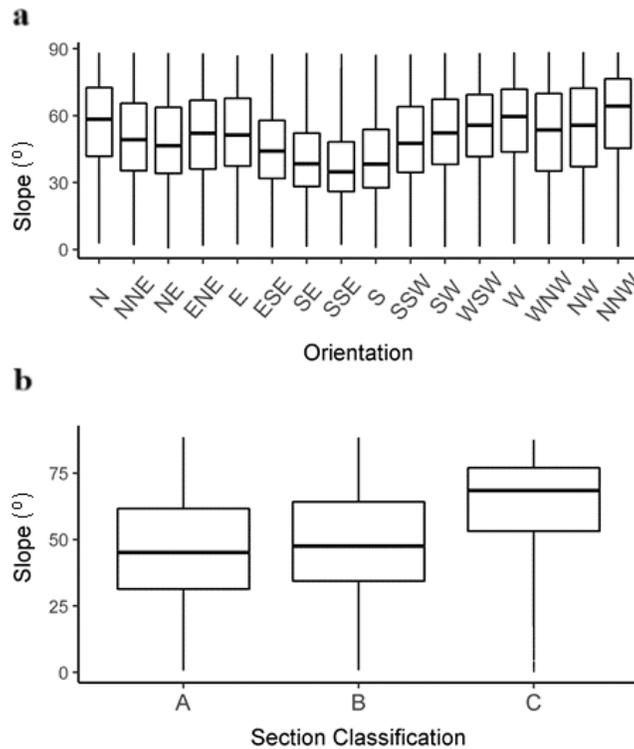


Figure 2. The guillemot survey sections and modelled air pressure on the cliffs of Skomer. a) The distribution of breeding guillemots. Areas classified as both densest and largest are indicated in red ($n = 7$ sections). Areas that were identified as either among the largest ($n = 3$) or densest ($n = 4$) are indicated in orange respectively. Residual occupied areas are indicated in yellow. b) Modelled air pressure at 2 m normal to the surface around Skomer for the SW wind direction (indicated with a black arrow). High pressure regimes are a feature of exposed cliffs, while pressure is lower in sheltered areas and over the main island.

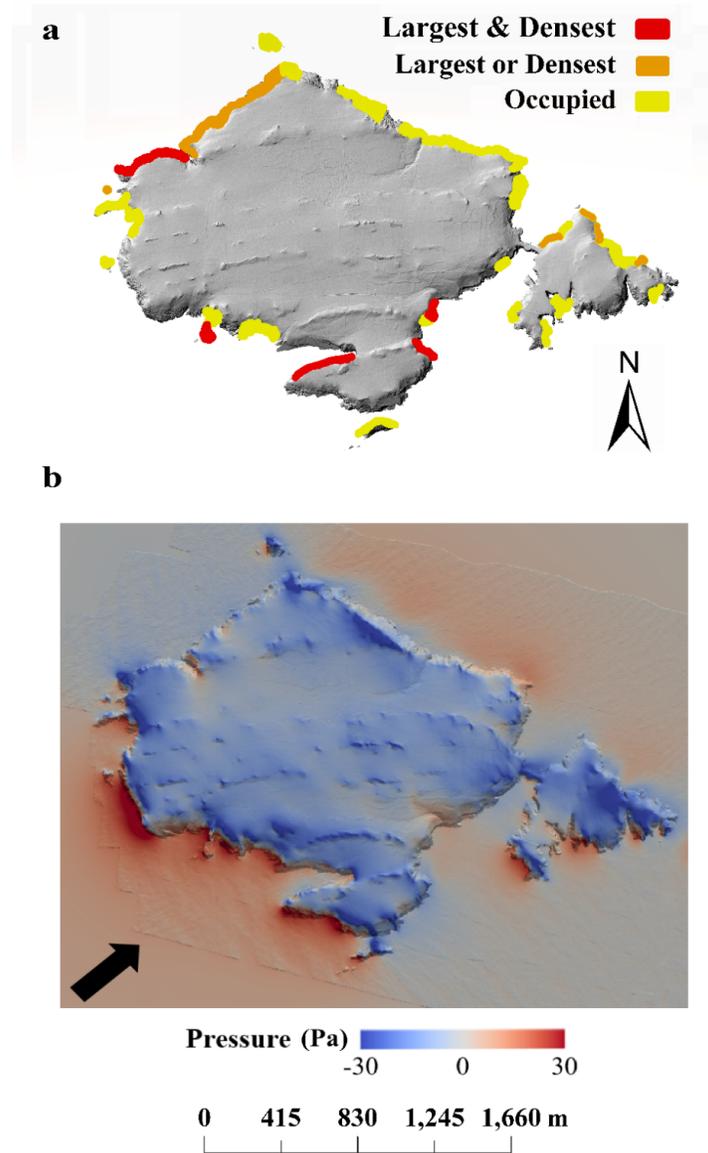


Figure 3. The OpenFoam model output of a) wind speed and b) pressure, over a windward cliff (“Skomer head”) with SW wind (denoted with black arrows). In the lower parts of the cliffs, the wind is blocked, resulting in high pressure regions where flow is decelerated. Closer to the top (55 - 60 m ASL), the flow is accelerated, generating areas of low pressure. This generates a wider range of pressures on windward cliffs, compared to leeward cliffs, where flow separation occurs, viscous forces take over, and areas of consistently low pressure are generated that are not associated with high wind speeds.

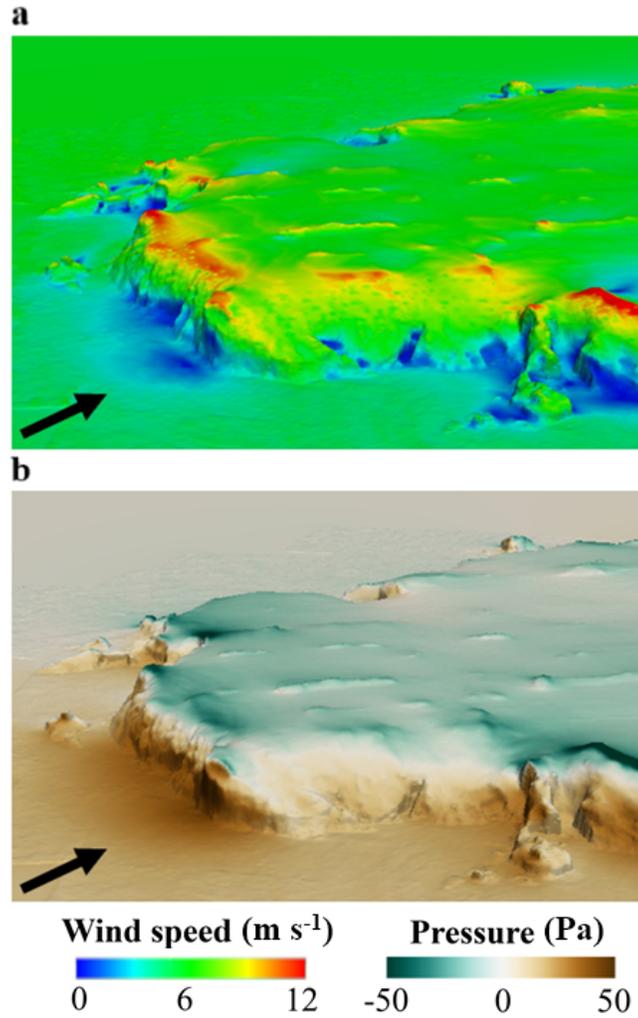


Figure 4 . Modelled horizontal wind speeds on the cliffs of Skomer. Modelled wind speeds under a) a SW and b) a NE wind direction. Mean wind speeds were reduced on leeward cliffs, increased on windward cliffs and reached their highest estimates at the crests, as expected. Winds were modelled 2 m normal to the surface and the mapped area was constrained by the 4 m and 40 m elevation contours.

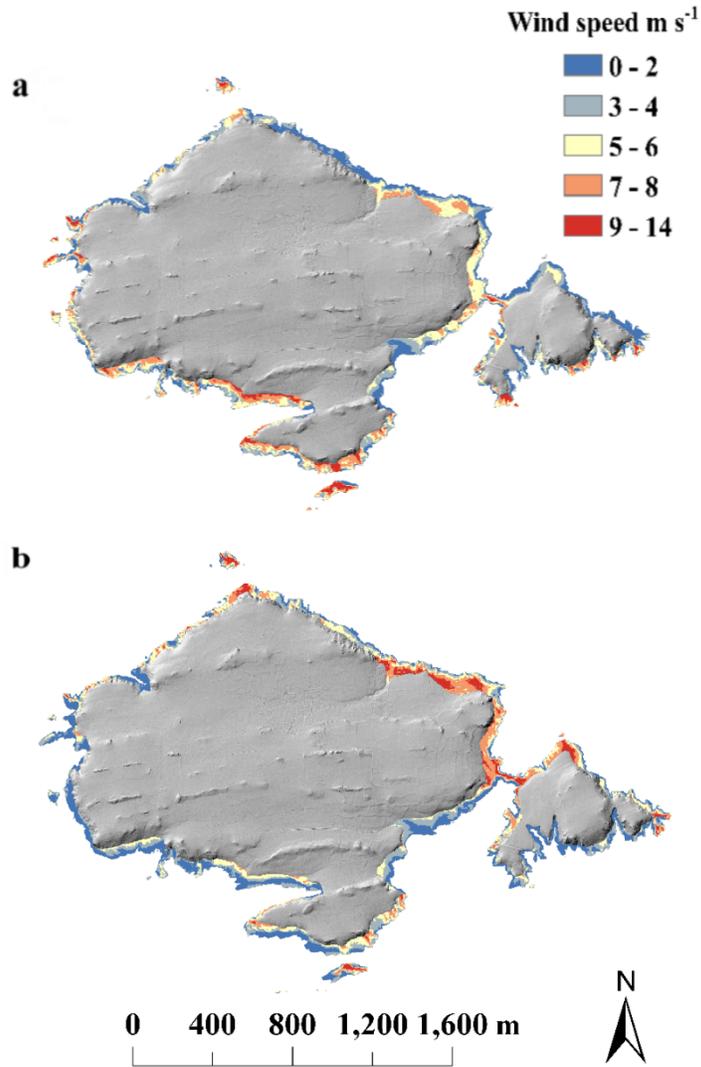


Figure 5. Predicted distribution of guillemot colonies on Skokholm. The distribution was predicted using the model of the largest colonies on Skomer and the wind field on Skokholm as predicted under the prevailing SW wind.

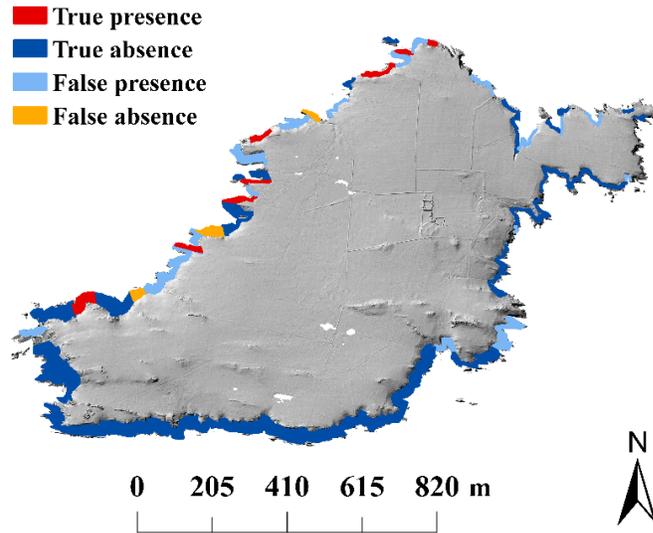


Table 1 . The outputs of logistic regression models predicting colony presence for four different initial wind directions. Three summary statistics were modelled for each section and wind property: “skewness” (Skew); “median” (Med) and “interquartile range” (IQR). In addition, three colony classifications were tested, where colony presence was taken as i) any positive count, ii) the 10 largest colonies and iii) the 11 densest colonies. Shelter from higher wind speeds is associated with low pressure (PMed) and reduced pressure range (PIQR). Exposure to higher wind speeds is highlighted by negative and decreased skewness in horizontal wind speed. Higher turbulence is indicated by increased TKE median and low TKE skewness. TI terms follow the same pattern. Significance is indicated according to p-value: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.005$ (*), and model predictors are listed in order of descending effect size (Supplementary Table 2).

Colony definition	SW				NW			SE			NE		
	Term	P-value / Significance	Est.	Term	P-value / Significance	Est.	Term	P-value / Significance	Est.	Term	P-value / Significance	Est.	
Any count	PMedian	< 0.001 ***	-2.27	TISkew	< 0.01 **	-1.94	TKEIQR	< 0.05 *	-1.66	TKESkew	< 0.001 ***	-4.39	
	TISkew	< 0.05 *	-1.54	TKESkew	< 0.01 **	-2.27	MeanSlope	< 0.01 **	+0.09	MeanSlope	< 0.001 ***	+2.80	
	MeanSlope	< 0.05 *	+1.49							HorizontalMedian	< 0.01 **	+2.12	
10 Largest	PIQR	< 0.05 *	-6.23	TKESkew	< 0.01 **	-3.36	MeanSlope	< 0.001 ***	+0.18	TKEIQR	< 0.01 **	+7.75	
	HorizontalIQR	< 0.01 **	+5.65	MeanSlope	< 0.01 **	+0.13				HorizontalSkew	< 0.05 *	-7.26	
	MeanSlope	< 0.001 ***	+4.08							MeanSlope	< 0.01 **	+4.53	
11 Densest	PMedian	< 0.05 *	-2.50	TKESkew	< 0.05 *	-2.31	MeanSlope	< 0.05 *	+0.10	TKEMedian	< 0.01 **	+8.27	
				MeanSlope	< 0.05 *	+0.10				U_2Median	< 0.01 **	-4.23	
										HorizontalSkew	< 0.05 *	-3.34	
McFadden pseudo R² – OA/ TSS/ Sensitivity/ Specificity													
Any count	0.28 – 0.66/ 0.32/ 0.63/ 0.69				0.24 – 0.63/ 0.21/ 1.00/ 0.21			0.12 – 0.56/ 0.18/ 0.21/ 0.96			0.38 – 0.71/ 0.45/ 0.60/ 0.84		
10 Largest	0.59 – 0.90/ 0.73/ 0.80/ 0.93				0.58 – 0.86/ 0.81/ 1.00/ 0.81			0.32 – 0.86/ 0.60/ 0.70/ 0.90			0.74 – 0.97/ 0.90/ 0.90/ 1.00		
11 Densest	0.17 – 0.65/ 0.48/ 0.90/ 0.57				0.40 – 0.84/ 0.78/ 1.00/ 0.78			0.15 – 0.72/ 0.51/ 0.81/ 0.69			0.67 – 0.88/ 0.84/ 1.00/ 0.84		