


# Factors determining nest-site selection of surface-nesting seabirds: a case study on the world's largest pelagic bird, the Wandering Albatross (*Diomedea exulans*)

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Several factors may drive bird nest-site selection, including predation risk, resource availability, weather conditions and interaction with other individuals. Understanding the drivers affecting where birds nest is important for conservation planning, especially where environmental change may alter the distribution of suitable nest-sites. This study investigates which environmental variables affect nest-site selection by the Wandering Albatross *Diomedea exulans*, the world's largest pelagic bird. Here, wind characteristics are quantitatively investigated as a driver of nest-site selection in surface-nesting birds, in addition to several topographical variables, vegetation and geological characteristics. Nest locations from three different breeding seasons on sub-Antarctic Marion Island were modelled to assess which environmental factors affect nest-site selection. Elevation was the most important determinant of nest-site selection, with Wandering Albatrosses only nesting at low elevations. Distance from the coast and terrain roughness were also important predictors, with nests more generally found close to the coast and in flatter terrain, followed by wind velocity, which showed a hump-shaped relationship with the probability of nest occurrence. Nests occurred more frequently on coastal vegetation types, and were absent from polar desert vegetation (generally above *c.* 500 m elevation). Of the variables that influence Wandering Albatross nest location, both vegetation type and wind characteristics are likely to be influenced by climate change, and have already changed over the last 50 years. As a result, the availability of suitable nest-sites needs to be considered in light of future climate change, in addition to the impacts that these changes will have on foraging patterns and prey distribution. More broadly, these results provide insights into how a wide range of environmental variables, including wind, can affect nest-site selection of surface-nesting seabirds.

**Keywords:** generalized additive model, generalized linear model, topography, vegetation type, wind.

Nest-site selection by birds may be driven by a variety of environmental factors, including habitat conditions related to predator avoidance, trophic

and non-trophic resource availability, exposure to weather conditions and interactions with conspecifics (Jones 2001). For example, many ground-nesting birds choose sites based on topography that allows them to either detect predators from afar (e.g. open areas) or those that provide protection from predators (e.g. less accessible sites within

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wetlands; Colwell *et al.* 2011, Miller *et al.* 2014, Cunningham *et al.* 2016, Korne *et al.* 2020). Vegetation is also regularly linked to the avoidance or detection of predators (Muir & Colwell 2010), and is often important in determining where nests are constructed (Flemming *et al.* 2019). Food availability is another key factor that is often linked to vegetation, and that can influence nest-site selection by bird species (McCollin 1998). Social cues, both inter- and intra-specific, can also affect the choice of breeding sites in songbirds (Betts *et al.* 2008). Temperature tends to be an important driver of nest-site selection, particularly in systems that experience high levels of solar radiation, with nests typically located in cooler microsites within hot environments (With & Webb 1993, Kauffman *et al.* 2021), and probably in buffered microsites in cold environments. Quantifying and understanding these factors is important in order to preserve environments that will be suitable for nesting in the future, and to understand how populations will be affected by environmental change.

Wind conditions may affect where birds choose to nest, but the influence of wind has been poorly studied (see, for example, Cunningham *et al.* 2016). Wind has been hypothesized to be important for nest location in certain specific scenarios, where, for example, nests are constructed downwind from taller vegetation, which may act as a windbreak (Holmes *et al.* 2020). Similarly, microscale tundra features in the Arctic may be important factors influencing shorebird nest-site location, because these landforms provide windbreaks (Cunningham *et al.* 2016). In other systems, the windward sides of nests have trampled vegetation where the birds enter the nest (Miller *et al.* 2014). Common Guillemots *Uria aalge* (Alcidae), a cliff-breeding seabird, nest in areas that are protected from wind and rain and waves, which are also affected by the wind characteristics (Lempidakis *et al.* 2022). Wind is being recognized as an important factor for seabirds, affecting their movement (Weimerskirch *et al.* 2000, Clay *et al.* 2020), foraging ecology (Cornioley *et al.* 2016), predation (Gilchrist & Gaston 1997) and even life-history (Weimerskirch *et al.* 2012). Large seabirds breeding on sub-Antarctic islands are an ideal system in which to study the influence of wind on the nest-site selection of surface-nesting species. In these environments, natural predators are absent (although predation by giant petrels *Macronectes*

spp. may occur; Dilley *et al.* 2013), proximity to food should not be a factor because these birds typically cover extremely large distances to forage (Gaston 2004), winds are constant and strong, and, therefore, environmental effects can be studied without the interference of predator risk or resource availability, which affect bird nesting sites strongly in other systems.

The Procellariiformes is a large order of seabirds, including the bird with the largest wingspan, the Wandering Albatross *Diomedea exulans* (Diomedidae), an oceanic nomad that only visits land to breed, and nests exclusively on the islands in the Southern Ocean (ACAP 2009). Wandering Albatrosses are long-lived birds (up to at least 57 years) that breed in loose colonies. They build large raised mound nest structures from surrounding vegetation and peat (Tickell 2000), having large, but very localized, impacts on the terrestrial ecosystem where they nest (Joly *et al.* 1987). Their nests tend to be in open, flat areas, with breeding pairs exhibiting high fidelity rates, almost always returning to the same site (Gauthier *et al.* 2010). Although not tested, it has been hypothesized that differences in breeding success on islands could be linked to environmental conditions, in particular shelter from westerly winds (Rackete *et al.* 2021).

The global population of Wandering Albatross is declining, mainly as a result of bycatch in long-line fishing, and the species is currently listed as Vulnerable (Poncet *et al.* 2017, Birdlife International 2018). Several threats to Wandering Albatross populations are well documented and understood (see Jones & Ryan 2010, Pardo *et al.* 2017, Jones *et al.* 2019), but factors affecting nest-site selection, and what this would mean for the distribution and availability of future breeding sites, have not been investigated. Wandering Albatross foraging patterns, breeding success and survival are affected by wind in different ways (Weimerskirch *et al.* 2000, 2012, Cornioley *et al.* 2016, Pardo *et al.* 2017). As a result of their large wingspan and heavy weight, energy expenditure is largest for these birds when they take off (Weimerskirch *et al.* 2000). Wandering Albatrosses take off into strong headwinds, and larger albatrosses, which have a higher wing loading and require higher wind speeds for gliding flight, are more strongly influenced by favourable wind conditions when making flight decisions (Clay *et al.* 2020).

This study investigates which environmental drivers affect nest-site selection among Wandering Albatrosses, and also, for the first time, quantitatively investigates wind as one of these factors. We expect that Wandering Albatross nests will be located in flat areas with adequate vegetation cover to build their nests that have adequate space for the birds to take off into the predominant winds, and which have moderate and predictable wind speeds to facilitate take-off and landing. We test these patterns using data from three breeding seasons to determine their generality.

## METHODS

### Study area

This study was conducted on sub-Antarctic Marion Island (46°54'S, 37°45'E; 293 km<sup>2</sup>), in the Prince Edward Islands group, southeast of Africa. Marion Island is situated in the 'roaring forties', a band of strong westerly winds in the Southern Ocean, where strong winds blow on most days of the year, with winds predominantly coming from the west (le Roux 2008). The island has a hyper-oceanic climate, where the Southern Ocean moderates daily and seasonal temperature variation (mean annual temperature of 6 °C, mean daily temperature range of 1.9 °C). The island receives around 1800 mm of precipitation annually, with rain or snow falling on more than 290 days per year (1960–2018, South African Weather Service unpublished data, le Roux 2008, le Roux & McGeoch 2008a). Vegetation on Marion Island can broadly be described as tundra, with similarities to the tundra systems in the northern hemisphere (Kemppinen *et al.* 2021).

### Data collection

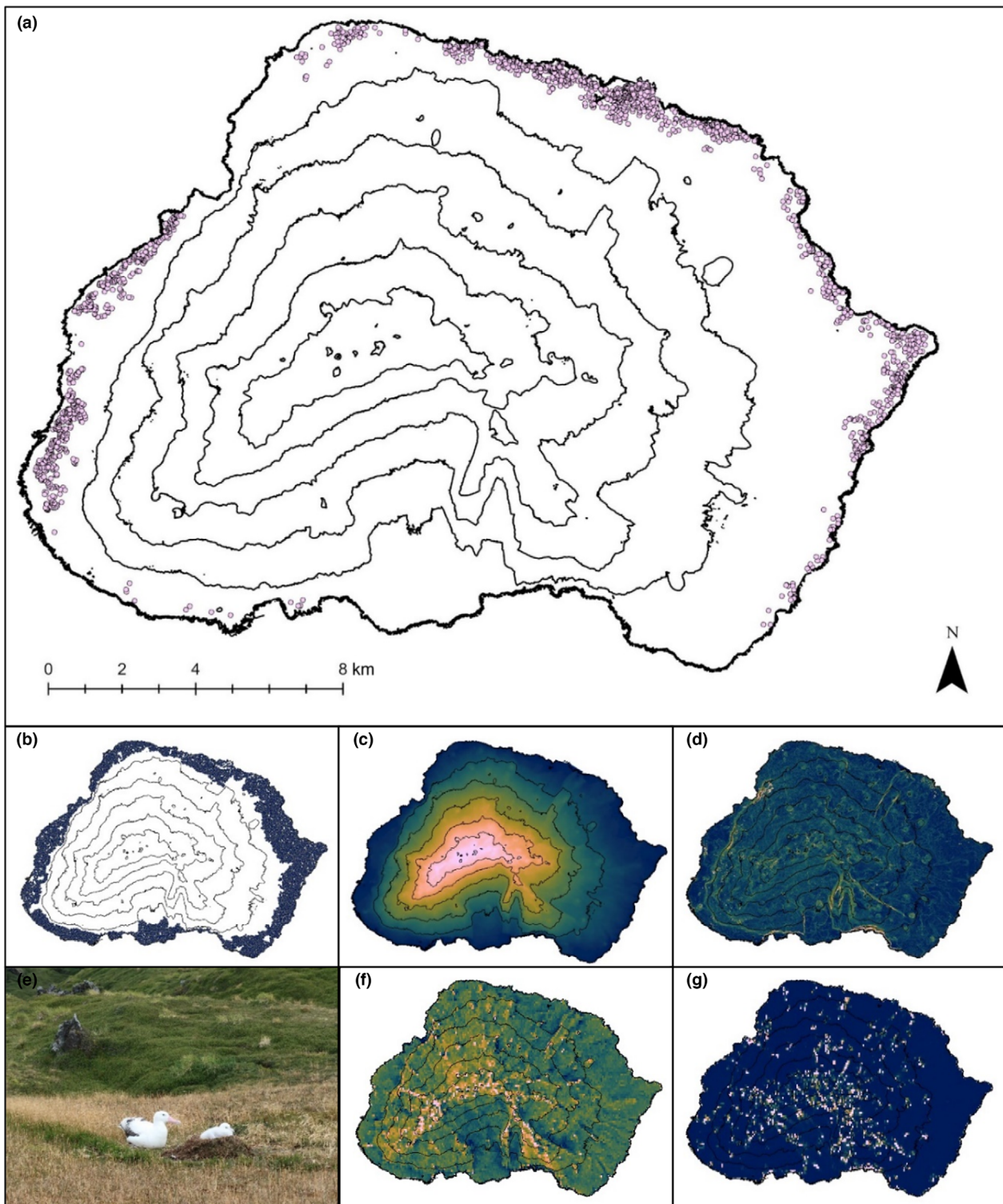
The geographical coordinates of 1906 of 1952 active Wandering Albatross nests on Marion Island (97.6% of all active nests in the 2016/17 breeding season; Fig. 1, after removing four outliers at elevations higher than 100 m above sea level (asl) and records that included errors in locations or lacked coverage by the digital surface model) were collected using a handheld GPS device (following the methods of Nel *et al.* 2002) in January 2017. Nest detection rate is very high because of the short vegetation (generally <0.1–0.2 m) and the large size and white plumage of Wandering

Albatrosses (adults and chicks). In addition, nests tend to be in the same areas each year, and the entire island is systematically searched for nests each year. Active nests from the 2006 (1711 nests) and 2018 (2139 nests) breeding seasons were used to confirm the generality of results across years. This provides a test of the generality of observed patterns, with data more than 10 years apart, and data from a subsequent breeding season representing the nesting preferences of different individual birds (as Wandering Albatrosses generally breed every second year, although, because of the longevity of this species or failed nest attempts in one year leading to breeding again in the subsequent year, not all records are independent).

### Data processing

Absences ( $n = 10\ 000$ ) were randomly generated in ArcGIS Pro, with a minimum distance of 30 m between all absence points and between any absence point and a nest location.

The island is surveyed intensively, so all locations that were recorded as not having an active nest represent true absences for that particular breeding season (see Guillera-Arroita *et al.* 2015). Models using pseudo-absences sampled from environments that are dissimilar to the environments in which presences occur may be positively biased (Hazen *et al.* 2021), so absences were a priori generated in areas that were deemed biologically suitable based on initial observations of where nests occur. The following factors were considered when choosing where to generate absences: nests occurred at elevations lower than 100 m asl, and the species does not nest on cliffs, because of their lack of agility when landing. Marion Island has over 130 scoria (cinder) cones (Boelhouwers *et al.* 2008) comprising loose unconsolidated rock resulting from explosive volcanic events (Verwoerd 1971, Rudolph *et al.* 2021). This geology type typically supports little to no vegetation and scoria cones are also generally very steep (see Holness 2004, with measurements of up to 35°), and Wandering Albatrosses have not been observed to nest on these cones. As scoria (cinder) cone vegetation was represented by only one nest in the dataset, this vegetation type was lumped with polar desert because both of these vegetation types represent abiotically extreme environments. Therefore, absences were not generated from areas with



**Figure 1.** (a) Map of Marion Island with 200-m contour lines and the 1906 georeferenced Wandering Albatross nests recorded in January 2017 (light pink points); (b) 10 000 randomly generated absences (dark blue); (c) digital surface model; (d) terrain ruggedness index; (e) Wandering Albatross parent and chick on nest; (f) wind velocity (m/s); (g) wind turbulence. For all maps, lighter colours indicate higher values and darker colours indicate lower values. See Supporting Information Figures S2–S7 for larger images, including legends and scales.



an altitude greater than 100 m asl, slopes greater than 45°, scoria cones or lakes.

The elevation for each presence and absence point was extracted from a 1-m resolution digital surface model (Fig. 1c; DRDLR 2019). Temperature and elevation show strong collinearity on Marion Island (Leihy *et al.* 2018), and therefore temperature was not included as a predictor. The digital surface model was subsequently resampled to 10-m resolution, using bilinear interpolation, before calculating and extracting the terrain ruggedness index (TRI) and slope angle in ArcGIS Pro. The TRI represents the elevation difference between a cell and the eight cells surrounding it, and was used as a proxy for the flatness of the space around each point, hereafter referred to as terrain roughness (rugosity). This indicated the available space that the birds would be able to use for take-off and landing (Fig. 1d).

Distance to the coast was calculated because salt spray from the ocean might affect nest-site selection, and salt spray can travel as far as 300 m inland on Marion Island (Smith 1978a). The vegetation type at each point was determined from the latest vegetation classification for Marion Island, which mapped five broad vegetation types: coastal vegetation, mire-slope vegetation, fellfield, scoria (cinder) cones and polar desert (Smith & Mucina 2006). Geology for each point was determined from Rudolph *et al.* (2021), and then simplified to two categories, namely flows from before the last glacial maximum (pre-glacial flows), which represent a smooth substrate, and post-glacial flows that are more rugged.

The weighted mean wind velocity and wind turbulence intensity were extracted from a computational fluid dynamics model of Marion Island (30-m resolution; Goddard *et al.* 2022). These mean values were weighted by the observed frequency of wind recordings (see Supporting Information, Fig. S1) from 16 wind directions (recorded over 2 years; 2018 and 2019). The computational fluid dynamics model uses the full digital surface model of Marion Island and simulates air flow over the topography by iteratively solving a set of partial differential equations (Reynolds-Averaged Navier Stokes Equations: Versteeg & Malalasekera 2007, Cindori *et al.* 2018). Sixteen wind directions (at intervals of 22.5°) were used as the free-stream condition, with a reference speed of 8.22 m/s at 1 m above ground (based on the average wind velocity across all 17 anemometers).

The model included considerations for the atmospheric boundary layer and the effect of the Coriolis force (Breedt *et al.* 2018, Goddard *et al.* 2022), and generated estimates of wind velocity and turbulence for 30 × 30-m cells across Marion Island (with mean errors of 26.9% for velocity and 32.6% for turbulence; Goddard *et al.* 2022). From these analyses, we extracted wind characteristics at 1 m above the ground because we considered this relevant to adult albatrosses when on the ground and chicks on nests. Outliers for wind turbulence, representing values greater than the value of the 99th centile, were set to the value of the 99th centile.

### Statistical analyses

The terrain roughness and wind turbulence values were logarithmically transformed before analyses to reduce the leverage of a few large values. Slope and roughness were strongly correlated (Pearson  $r = 0.86$ ,  $P < 0.001$ ), so slope was excluded from the analyses because roughness was considered to be more biologically relevant in terms of quantifying the available flat space around a point for take-off and landing. None of the remaining predictor variables had a generalized variance inflation factor greater than 2.5, and none was strongly correlated with another variable (Pearson  $r < |0.7|$ ; see Supporting Information, Fig. S8). Wind velocity, turbulence, vegetation type, elevation, geology, terrain roughness and distance from the coast were investigated as predictors of nest presence or absence using a generalized additive model (GAM) and a generalized linear model (GLM; including quadratic terms of continuous predictors), implementing a binomial distribution. These two differing statistical approaches were used to cross-check the results, providing higher confidence in the conclusions if/where consistent results were observed. Variable importance for GAMs and GLMs was calculated by comparing the Pearson correlation between predictions made on the original data and predictions made on the data where the predictor variable of interest has been randomly shuffled (following Niittynen & Luoto 2018). The calculations of variable importance were calculated 10 times and the mean importance value, rescaled to percentage, is reported.

All statistical analyses were performed in R version 4.1.0 (R Core Team 2021), using additional

functions from the `mgcv` (Wood & Augustin 2002), `ggplot2` (Wickham 2016), `voxel` (Garcia de la Garza *et al.* 2018), `ggpubr` (Kassambara 2020) and `scico` (Pedersen & Cramer 2020) libraries. All figures were produced using the scientific colour scheme `batlow` (Cramer 2018), to prevent visual distortion of the data and to be accessible to readers with colour-vision deficiency (Cramer *et al.* 2020).

## RESULTS

Wandering Albatrosses breed around most of the coast of Marion Island, but are largely absent from the south coast, and occur at the highest densities along the northeast coast (Fig. 1a). The results presented here are from the 2017 breeding season, but similar results were obtained from the 2006 and 2018 breeding seasons, with predictors consistently ranked in the same order of importance and with response curves showing similar shapes across all three datasets (see Supporting Information, Figs S9 and S10, and Tables S1 and S2 for results from these additional years). The spatial nature of the data means that spatial autocorrelation is present, but using a spatially thinned version of the data produced similar results (see Supporting Information, Table S3 for more information). The GAM explained 33.1% of the deviance in the 2017 nest distribution data, and the GLM explained 31.5% of the deviance.

Four of the five continuous predictors contributed significantly to explaining nest-site suitability in both the GAM and GLM, but wind turbulence did not significantly affect the nest-site suitability in either of the two models (Table 1). For both statistical approaches, elevation was the most important predictor, followed by distance from the coast, vegetation type, terrain roughness and wind velocity (Table 1). Most nests were located in coastal or mire-slope vegetation types, with a small proportion in fellfield; no nests were recorded in polar desert vegetation (Fig. 2). Pre-glacial flows made up a significantly larger proportion of the underlying geology on which nests were found than would be expected by chance, with a similar proportion of pre-glacial and post-glacial flows observed for absences (Fig. 2). Response curves from the GAMs showed that there was a higher probability of a nest occurring in areas close to the coast and at low elevation (Fig. 3). The more rugged the terrain, the lower

the probability of a site being used to build a nest. Wind velocity had a hump-shaped relationship with nest occurrence, with the highest probability of a nest in areas with intermediate wind velocities. Areas with higher wind turbulence generally had a smaller probability of containing a nest than areas with lower turbulence, although this relationship was not significant (Fig. 3).

## DISCUSSION

Predictor variables representing topographic, vegetation, geological and wind velocity characteristics were significantly related to Wandering Albatross nest locations in the tundra landscape of Marion Island, although the relative importance of these predictors varied strongly. The consistency in results across three different years indicates the generality in these findings (i.e. across different individuals and different time periods). Although adults and most juveniles demonstrate strong fidelity to their breeding/natal sites, there is sufficient dispersal of juveniles in particular to allow breeding sites to shift in response to local conditions (Inchausti & Weimerskirch 2002, Gauthier *et al.* 2010).

Despite the very windy conditions present at the study site, and the strong impacts on albatross flight patterns and feeding behaviour, wind velocity was only the fifth most important driver of nest-site selection in Wandering Albatrosses, after elevation, distance from the coast, vegetation type and terrain roughness. Wind velocity can affect birds and their nests in several ways. High wind speeds can greatly decrease nest temperatures (Heenan & Seymour 2012, Gray & Deeming 2017), and also affect the chick's body temperature, potentially reducing their growth rate (Sauve *et al.* 2021). Shorebirds have been found to adjust their directional orientation when resting in response to wind speed and ambient temperatures, allowing them to increase the efficiency of thermoregulation and save energy (Cestari & de Melo 2022). Protection from wind in general, or from the strongest winds at a site, have been theorized to impact where birds construct their nests based on topographic and vegetative protection (Cunningham *et al.* 2016, Holmes *et al.* 2020). Our study presents quantitative results for wind impacting bird nest-site selection, and shows that for the Wandering Albatross, nests were most likely to be constructed in areas of intermediate

**Table 1.** Significance and variable importance for all variables when predicting the presence or absence of a Wandering Albatross nest based on data from the 2018 breeding season

Predictor	GAM			GLM		
	$\chi^2$	<i>P</i> value	Relative importance (%)	$\chi^{2a}$	<i>P</i> value	Relative importance (%)
Elevation	478.60	< 0.001	46.87	21.6	0.005 <sup>b</sup>	42.94
Distance to coast	249.12	< 0.001	24.05	434.8	< 0.001 <sup>b</sup>	24.18
Vegetation type		<i>P</i> < <i>F</i> < <i>M</i> < <i>C</i>	16.15	356.79	<i>P</i> < <i>F</i> < <i>M</i> < <i>C</i>	15.79
Terrain roughness	127.30	< 0.001	6.37	54.58	0.003 <sup>b</sup>	8.69
Wind velocity	73.45	< 0.001	5.89	160.66	< 0.001 <sup>b</sup>	7.73
Geology type		Post < Pre	0.36	4.14	Post < Pre	0.23
Wind turbulence	2.54	0.078	0.30	2.91	0.34	0.44

GAM, generalized additive model; GLM, generalized linear model. The % deviance explained was 34.30% for the GAM and 32.85% for the GLM. An overall *P* value for categorical predictors was not reported from a GAM, so the ranking of the levels is reported.  $\chi^2$  values are not reported for categorical predictors in a GAM. Post—post-glacial flows, Pre—pre-glacial flows, P—sub-Antarctic polar desert, F—sub-Antarctic fellfield, M—sub-Antarctic mire-slope vegetation, C—sub-Antarctic coastal vegetation. <sup>a</sup> $\chi^2$  values for linear and quadratic terms of a predictor in the GLM were summed. <sup>b</sup>Quadratic term of that variable was significant in the GLM.

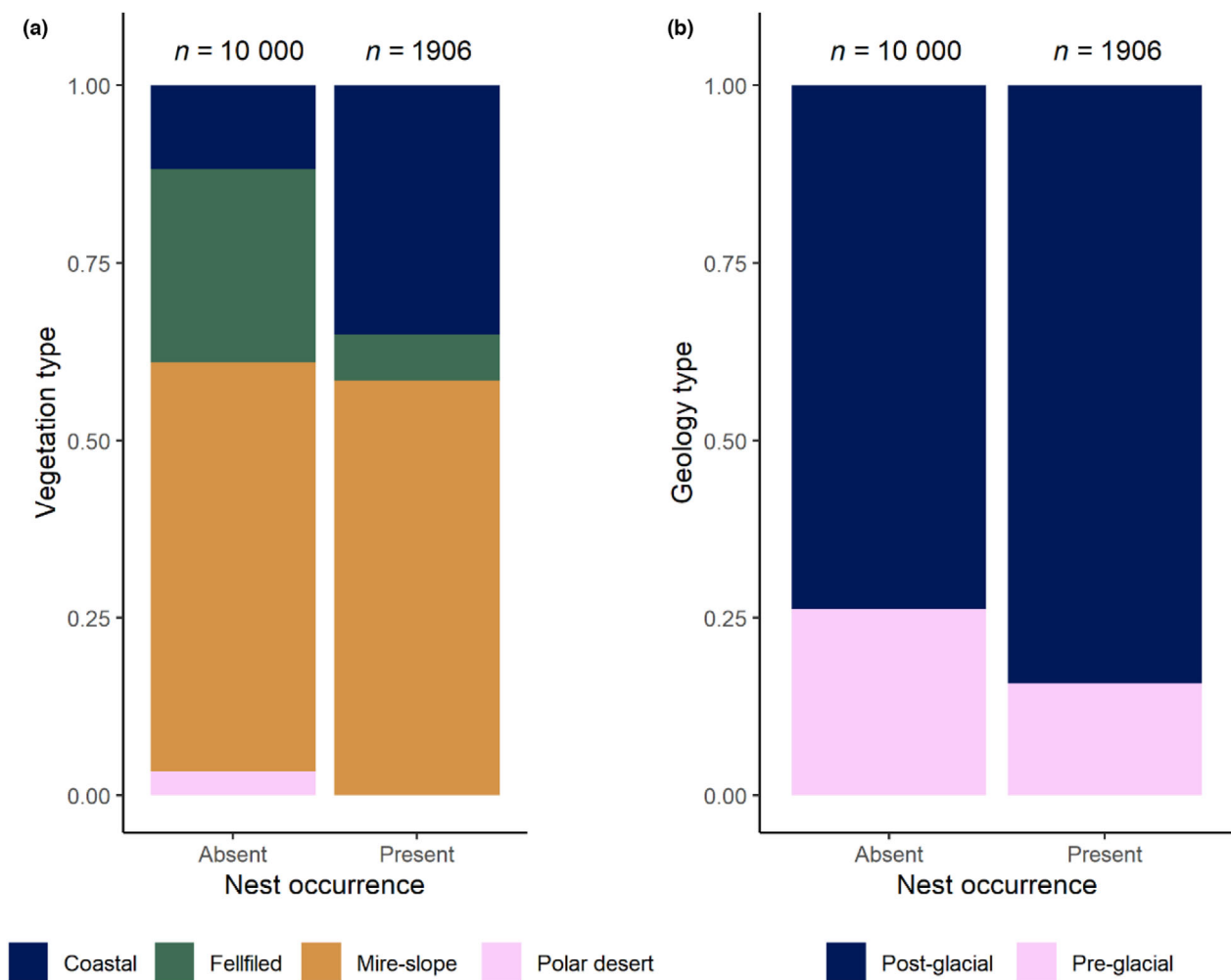
wind speeds. This is probably because this species needs strong enough wind speeds to take-off and land (making very wind-sheltered locations unsuitable), but also benefits from protection from the strongest wind speeds, both for thermoregulation and for chicks not to be blown off their nests. This influence of flight-related wind preferences impacting nest-site selection is in agreement with those for a cliff-nesting seabird species on much smaller islands, where Common Guillemots are only able to land in very low wind speeds, and therefore nest in more sheltered locations (Shepard *et al.* 2019, Lempidakis *et al.* 2022).

In addition to wind, other predictors explained even more of the variation in nest-site selection. Elevation was the most important predictor of Wandering Albatross nests, with the probability of encountering a nest decreasing rapidly above *c.* 25 m asl. Similar results have been seen for surface-nesting species in the Arctic, where low-elevation areas are important for 33 species of tundra-breeding birds (Hawkshaw *et al.* 2021). There is a strong negative correlation between elevation and temperature on Marion Island (Leihy *et al.* 2018), so lower elevations are warmer sites, protecting chicks from very low temperatures (although Wandering Albatross chicks are well insulated against the cold; Cooper & Lutjeharms 1992). Similarly, the probability of nests being present declined with distance from the coast (which could have impacts on thermal buffering), which typically correlates with elevation. This result is comparable to several studies

on Arctic birds, where higher numbers of birds are present in coastal habitats, probably as a result of the larger amounts of suitable habitat (e.g. wetlands or tidal habitats) available in these areas (Conkin & Alisauskas 2013, Saalfeld *et al.* 2013, Hawkshaw *et al.* 2021).

Vegetation type was the third most important predictor, and co-varies with elevation and distance from the coast, because some vegetation types are limited to areas receiving salt-spray (i.e. coastal vegetation) and others are limited to high altitudes (e.g. polar desert; Smith 1978b). High vegetation productivity (which on Marion Island declines with increasing elevation; Smith 2008) has previously also been linked to tundra bird abundance, as some birds use the vegetation cover for nesting, and others for foraging (Hawkshaw *et al.* 2021). The composition of vegetation surrounding the nest was also an important determinant of nesting site choice for several Arctic-breeding shorebirds, probably because of predator protection and invertebrate food sources (Cunningham *et al.* 2016), and adequate vegetation is needed to construct nests. Wandering Albatrosses may prefer low-elevation, coastal areas for nesting because these areas are warmer, and there is ample vegetation available with which to construct their nests.

Terrain roughness was also significantly related to nest occurrence, with areas that have a higher roughness having a lower chance of containing a Wandering Albatross nest, in line with our hypothesis. Terrain roughness has been shown to be an



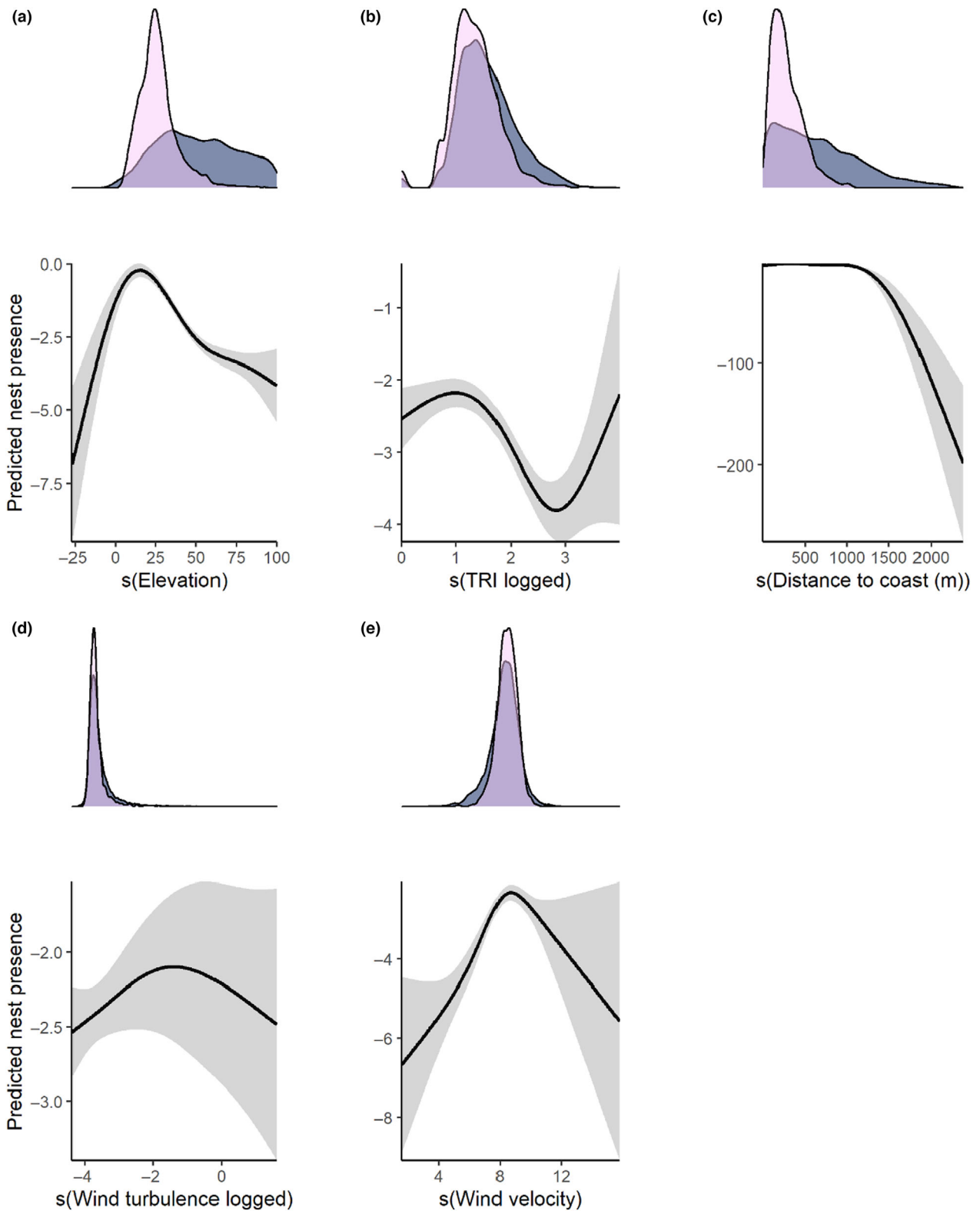
**Figure 2.** Stacked bar charts showing the proportion of nest presences and absences in each (a) vegetation type and (b) geology type. In (a), sub-Antarctic coastal vegetation—dark blue, sub-Antarctic fellfield—live green, sub-Antarctic mire-slope vegetation—orange, sub-Antarctic polar desert—light pink. In (b), post-glacial flows—dark blue, pre-glacial flows—light pink.

important driver of nest-site selection in other systems, where birds prefer to nest in areas with low terrain roughness in order to provide individuals with a greater field of view to detect predators (Korne *et al.* 2020). As Wandering Albatrosses have a high visibility in the landscape (because they are taller than almost all vegetation on the island), the mechanism through which this terrain roughness affects nest-site selection is probably

different (although predation by invasive House Mice *Mus musculus* has been recorded in recent years; Jones & Ryan 2010, Jones *et al.* 2019). Wandering Albatrosses need adequate flat space (i.e. low terrain roughness) during take-off and landing, because of their large size requiring longer 'runways' to achieve adequate speed before taking flight and to land safely (Warham 1977). For some other surface-nesting species, (micro-)relief can

**Figure 3.** Density plots of the raw data and generalized additive model response curves for the occurrence of Wandering Albatross nests for the 2017 breeding season, for (a) elevation, (b) terrain ruggedness index (logged), (c) distance to the coast, (d) wind turbulence (logged) and (e) wind velocity (m/s). Light pink density plots represent data from presences and dark blue density plots represent data from absences. In the response curves, larger values on the y-axis represent a higher probability of occurrence.





provide wind shelter for nesting birds, helping them to avoid excessive heat loss in windy conditions in the Arctic (Cunningham *et al.* 2016). However, for species that have chicks that stay on the nest throughout winter, these microsites could also allow for greater snow accumulation, which might offset the benefits that these sites provide in terms of wind shelter. This is probably also true for Northern Giant Petrels *Macronectes halli*, which nest adjacent to rocks or on the leeward side of vegetation, where they are sheltered from wind (Marchant *et al.* 1990). Here, however, we observe the opposite pattern for Wandering Albatross, where it appears that shelter is not as important as potential runway area. Topography and wind may be strongly linked at certain spatial scales, and although there is not a strong correlation between terrain roughness and wind velocity in this study, this relationship may change when investigated at different spatial scales. This result may not be universal and may depend on site-specific characteristics and/or spatial scale.

Wind turbulence and geology had weak impacts on the probability of a nest occurring at a site. Wind turbulence could have a limited effect on nest-site locations because these birds only nest just above ground level, and wind speed is lower at ground level, implying that wind turbulence, or 'gusting' occurs from a low underlying speed value. Nonetheless, the observed negative trend between turbulence and nest occurrence fits our expectation that Wandering Albatrosses would avoid areas of turbulent wind flow, as these areas may increase the risks of crashing during take-off or landing (although the influence of wind conditions on landing may need to be considered at broader scales because of the large distances, spanning different heights above the ground, required for landing). In terms of geology, pre-glacial deposits tend to be flatter and smoother, and, therefore, meet the requirements for long, flat 'runways' more closely than post-glacial flows. Anecdotally, this can be seen on the west coast of the island, where there are fewer nests, corresponding to large black lava flows. However, many of the post-glacial flows at low altitudes are vegetated and often occur under peat deposits, which evens out the underlying roughness, and leads to fewer biologically relevant differences for the Wandering Albatrosses between geology types. Pre-glacial deposits tend to have relatively less vegetation, but include depressions that are filled with peat. These

areas with peat deposits (regardless of the underlying geology) provide sufficient vegetation for Wandering Albatrosses to build their nests, suggesting that surface substrate may be more important than underlying geology in influencing nest-site selection in this species.

Predicting how nest-site availability might change under future conditions would probably be most dependent on vegetation and wind characteristics (wind speed, and possibly wind direction and wind turbulence), both of which are currently being affected by anthropogenically driven climate change. Changes to vegetation in relation to climatic changes have already been documented, with some species in the sub-Antarctic showing strong upslope range expansion, leading to community reorganization in some areas (le Roux & McGeoch 2008b), and others showing decreased survival because of increasing temperatures and lower precipitation (le Roux *et al.* 2005). These changes will affect the distribution of entire vegetation types and may, for example, increase the availability of vegetation for nest building at higher altitudes (improving the suitability of more inland areas as nesting sites). Wind speeds have increased globally over the past three decades, with the strongest increases observed in the Southern Ocean (Young *et al.* 2011, Young & Ribal 2019). As nest-site selection is influenced by wind velocity, anthropogenically driven shifts in climate could potentially affect the total suitable nesting area and, consequently, potentially the population's total breeding success via changes in wind characteristics. Small changes to wind velocity could create more suitable nesting sites for Wandering Albatrosses, but large increases may cause wind velocities to be too high for the birds to reliably land at nest-sites, thereby possibly leading to a reduction in potential suitable nest-sites. A factor that has not been quantified here, but that could potentially also have large impacts on suitable nest-sites and breeding success, is changes to the frequency of extreme wind events which can, for example, blow chicks off their nests.

Elevation and temperature are strongly correlated on Marion Island (Leihy *et al.* 2018), and elevation had the strongest influence on nest occurrence, so it is possible that changes to temperature could have a large effect on suitable nest locations. The sub-Antarctic islands, where Wandering Albatrosses and many other pelagic seabirds breed, have already experienced rapid climatic

changes (le Roux 2008). Temperature has increased at more than double the global average warming rate over the past 50 years, and annual precipitation has declined on several islands (le Roux 2008, le Roux & McGeoch 2008a). This change in temperature, specifically, might negatively affect Wandering Albatrosses, where high sea surface temperatures are detrimental to foraging success, and therefore adult survival in the breeding season (Pardo *et al.* 2017, see also Ventura *et al.* 2021 where increased sea surface temperatures led to higher divorce rates in Black-browed Albatrosses *Thalassarche melanophris*), which could alter where they nest in future. Altitudinal shifts in nesting sites could be a possibility, both as a result of increasing temperatures and the shift in vegetation as a result of temperature changes.

Other surface-nesting seabirds that breed in the sub-Antarctic, such as giant petrels (Ryan & Bester 2008), are likely to show similar patterns and experience analogous changes to suitable nesting locations in future. More generally, several other seabird species, for example skuas, shags, gulls and terns, all construct nests on the ground surface and occur in environments where wind speeds are relatively high (because of being close to the open ocean, Possner & Caldeira 2017, Schrimpf & Lynch 2021). Therefore, these results could provide insights into where surface-nesting seabirds nest in general, and how the availability of these sites will be affected by future climatic changes. More broadly, this work provides insights into wind as an underexplored climatic component of nest-site selection for surface-nesting seabirds, and is important for improving our predictions for climate change impacts on bird nesting habitat.

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## AUTHOR CONTRIBUTIONS

**Mia Momberg:** Conceptualization (equal); formal analysis (lead); methodology (equal); writing – original draft (lead). **Peter G. Ryan:** Methodology (equal); resources (equal); writing – review and editing (equal). **David W. Hedding:** Methodology (equal); writing – review and editing (equal).

**Janine Schoombie:** Resources (equal); writing – review and editing (equal). **Kyle A. Goddard:** Resources (equal); writing – review and editing (equal). **Ken J. Craig:** Resources (equal); writing – review and editing (equal). **Peter C. le Roux:** Conceptualization (equal); formal analysis (supporting); funding acquisition (lead); methodology (equal); writing – review and editing (equal).

## ETHICAL NOTE

None.

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## Data Availability Statement

Data are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Wind roses from four wind stations located on the north, east, west and south sides of Marion Island.

**Figure S2.** Locations of Wandering Albatross nests on Marion Island in January 2017.

**Figure S3.** Locations of absence points generated on Marion Island based on the nest locations from January 2017.

**Figure S4.** Digital Surface Model of Marion Island.

**Figure S5.** Terrain Ruggedness Index values across Marion Island.

**Figure S6.** Wind velocity on Marion Island.

**Figure S7.** Wind turbulence intensity on Marion Island.

**Figure S8.** Correlation matrix between continuous predictor variables.

**Figure S9.** Generalized additive model response curves for the occurrence of Wandering Albatross nests based on data from the 2006 breeding season.

**Figure S10.** Generalized additive model response curves for the predicted presence of Wandering Albatross nests based on data from the 2018 breeding season.

**Table S1.** Significance and variable importance for all predictor variables when modelling the presence or absence of Wandering Albatross nests based on data from the 2006 breeding season.

**Table S2.** Significance and variable importance for all variables when predicting the presence or absence of a Wandering Albatross nest based on data from the 2018 breeding season.

**Table S3.** Significance and variable importance for all predictor variables when modelling the presence or absence of Wandering Albatross nests based on spatially thinned data from the 2017 breeding season.