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# Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird

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## Abstract

1. In a highly dynamic airspace, flying animals are predicted to adjust foraging behaviour to variable wind conditions to minimize movement costs.
2. Sexual size dimorphism is widespread in wild animal populations, and for large soaring birds which rely on favourable winds for energy-efficient flight, differences in morphology, wing loading and associated flight capabilities may lead males and females to respond differently to wind. However, the interaction between wind and sex has not been comprehensively tested.
3. We investigated, in a large sexually dimorphic seabird which predominantly uses dynamic soaring flight, whether flight decisions are modulated to variation in winds over extended foraging trips, and whether males and females differ.
4. Using GPS loggers we tracked 385 incubation foraging trips of wandering albatrosses *Diomedea exulans*, for which males are *c*. 20% larger than females, from two major populations (Crozet and South Georgia). Hidden Markov models were used to characterize behavioural states—directed flight, area-restricted search (ARS) and resting—and model the probability of transitioning between states in response to wind speed and relative direction, and sex.
5. Wind speed and relative direction were important predictors of state transitioning. Birds were much more likely to take off (i.e. switch from rest to flight) in stronger headwinds, and as wind speeds increased, to be in directed flight rather than ARS. Males from Crozet but not South Georgia experienced stronger winds than females, and males from both populations were more likely to take-off in windier conditions.
6. Albatrosses appear to deploy an energy-saving strategy by modulating taking-off, their most energetically expensive behaviour, to favourable wind conditions. The

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behaviour of males, which have higher wing loading requiring faster speeds for gliding flight, was influenced to a greater degree by wind than females. As such, our results indicate that variation in flight performance drives sex differences in time–activity budgets and may lead the sexes to exploit regions with different wind regimes.

**KEYWORDS**

biologging, foraging behaviour, hidden Markov model, movement ecology, niche specialization, optimization, sexual segregation, wandering albatross

## 1 | INTRODUCTION

Optimal foraging theory predicts that foraging animals should adjust their behaviour to maximize both time and energy efficiency (Pyke, 1984; Stephens, Brown, & Ydenberg, 2008; Ydenberg, Welham, Schmid-Hempel, Schmid-Hempel, & Beauchamp, 1994). Over the course of a foraging trip, individuals must make a number of movement decisions, including when and where to forage, which route to take and how fast to travel (Alerstam & Lindström, 1990; Hedenström & Alerstam, 1995; Shamoun-Baranes, Liechti, & Vansteelant, 2017; van Loon, Shamoun-Baranes, Bouten, & Davis, 2011). Analogous to the distribution of resources (MacArthur & Pianka, 1966), the movement costs associated with acquiring them are often unevenly distributed in space and time (Gallagher, Creel, Wilson, & Cooke, 2017; Wilson, Quintana, & Hobson, 2012). For flying animals, the medium (air) through which they move is highly dynamic, influenced by fronts and other pressure changes, and with winds that vary in strength and directionality across a range of timescales (from seconds to decades; Shamoun-Baranes et al., 2017). Through direct effects on flight efficiency wind plays a crucial role in determining the energy (Elliott et al., 2014; Shepard et al., 2013) and time–activity budgets of foraging animals (Alerstam & Lindström, 1990). However, the extent to which movement decisions along foraging trips, such as when to forage or rest, are modulated according to the variable wind encountered, is not well understood (Harel et al., 2016; Shepard, Vallmitjana, Lambertucci, & Wilson, 2011).

Large soaring birds are particularly well-adapted to exploit a dynamic airspace (Hedenström, 1993; Richardson, 2011; Shepard, Williamson, & Windsor, 2016), extracting kinetic energy from wind for soaring–gliding flight (Pennycuick, 1982, 1998). This substantially reduces time spent flapping, which is metabolically costly compared with gliding (Duriez et al., 2014; Weimerskirch, Guionnet, Martin, Shaffer, & Costa, 2000). Their large wingspans and high wing loading (mass per unit wing area) enable rapid flight speeds through the air, and some species, particularly seabirds, travel vast distances in search of patchily distributed prey (MacArthur & Pianka, 1966; Weimerskirch, Gault, & Cherel, 2005). However, unfavourable or unpredictable winds can increase time and energy costs of movement (e.g. Harel et al., 2016; Horvitz et al., 2014). Activities such as taking-off, which requires intense flapping flight, are energetically demanding in windless conditions (Duriez et al., 2014; Weimerskirch et al., 2000), so individuals are predicted to modulate decision-making so that these activities are assisted by wind (Alarcón et al., 2017; Harel et al., 2016; Shamoun-Baranes et al., 2017). However, if birds have to wait for favourable conditions, they inevitably miss foraging opportunities. Ultimately, the sequence of movement decisions determines the success of a foraging trip, with downstream effects on individual fitness and population dynamics (Nathan et al., 2008).

Individual variation in morphology and its effects on flight performance may lead to divergent behavioural responses to environmental conditions (e.g. Barbraud, Weimerskirch, Robertson, & Jouventin, 1999; Clay, Oppel, Lavers, Phillips, & M. deL. Brooke., 2019; Spear & Ainley, 1997a). Sexual size dimorphism is widespread in soaring birds and foraging strategies often differ between sexes as a result of size-mediated competitive exclusion or niche divergence (González-Solís, Croxall, & Wood, 2000; Phillips, Silk, Phalan, Catry, & Croxall, 2004; Ruckstuhl & Neuhaus, 2005; Wearmouth & Sims, 2008). As body size has a functional influence on flight, differences in performance are expected (Møller, 1991; Shaffer, Weimerskirch, & Costa, 2001). For sexually dimorphic albatrosses, whereby males are often around 20% larger than females and have greater wing loading requiring faster speeds for gliding flight (Pennycuick, 1982; Shaffer et al., 2001), males attain faster speeds through the air on foraging trips (Wakefield et al., 2009). Males often, but not exclusively, forage further south than females (e.g. Phillips et al., 2004; Weimerskirch, Salamolard, Sarrazin, & Jouventin, 1993), where in the Southern Ocean mean wind speeds are stronger on average. The proximate role of wind in determining spatial distributions is debated (Phillips et al., 2004; Shaffer et al., 2001; Wakefield et al., 2009), and it remains unclear whether males and females differ in flight decisions in response to wind conditions, with implications for time–activity budgets and relative energy expenditure.

We investigated the extent to which wind shapes the movement decisions of a sexually dimorphic soaring seabird, the wandering albatross *Diomedea exulans*, and whether males and females respond to wind differently. Foraging trips of incubating birds can last up to around 30 days and often take the form of loops, following prevailing wind patterns regimes at ocean-basin scales (Jouventin & Weimerskirch, 1990; Murray, Nicholls, Butcher, & Moors, 2003; Weimerskirch et al., 2000). Over fine scales (metres and seconds), birds conduct zig-zag dynamic soaring flight taking advantage of wind velocity gradients close to the sea surface (Richardson, 2011; Sachs, 2005). Over larger scales (kilometres and minutes, or hours), movements can be split into bouts

of long directed flight at high speeds (relocating between foraging patches), interspersed with sinuous flight associated with searching for prey (Pinaud & Weimerskirch, 2005), and periods of sitting on the water (Phalan et al., 2007; Weimerskirch, Wilson, & Lys, 1997). At this scale their movements are predominantly thought to reflect the distribution of prey patches (Weimerskirch et al., 2005), yet movement decisions may also reflect hourly to daily changes in winds, related to the passage of low pressure weather systems.

We tracked males and females during incubation from two major populations, the Crozet Islands (southwest Indian Ocean), and South Georgia (southwest Atlantic Ocean). Both are in some of the windiest oceanic regions on Earth; yet, wind speeds are stronger around Crozet than South Georgia (Wakefield et al., 2009; Weimerskirch, Louzao, de Grissac, & Delord, 2012). We first tested whether birds from different populations and sexes experienced different wind conditions during foraging trips. We then used hidden Markov models (HMMs) to identify behavioural states (i.e. directed flight, area-restricted search and rest) from movement data and model the effects of wind speed and direction, and sex, on the probability of changing state, representing decision-making by foraging animals (Patterson, Basson, Bravington, & Gunn, 2009). We hypothesized that if birds pursued an energy-saving strategy, they should adjust their behaviour according to the wind conditions they encounter, such that wind speed and direction influence the probability of changing state. In particular, as taking-off is the most energetically expensive behaviour (Weimerskirch et al., 2000), birds should switch from rest to flight coincident with favourable (i.e. high) wind speeds ($H_1$). When in flight, wind speed and direction should influence the degree to which birds conduct prey search or more directed travel. Optimal foraging theory predicts that when travelling between foraging patches, birds should minimize movement costs (Hedenström & Alerstam, 1995) and preferentially use crosswinds and tailwinds to maximize ground speeds (Spear & Ainley, 1997b; Wakefield et al., 2009; Weimerskirch et al., 2000); in contrast, optimal flight speeds should be lower when searching for prey to facilitate prey detection (Alerstam, Gudmundsson, & Larsson, 1993; Hedenström & Alerstam, 1995). As such, we predict that increases in wind speeds and a greater similarity between wind and bird directions, should favour directed flight over ARS ($H_2$). Lastly, due to sex differences in flight performance (Shaffer et al., 2001), we predict that behavioural responses of males will be more strongly influenced by wind. Specifically, due to their higher wing loading, males should both remain in directed gliding flight, and be more likely to take off in stronger winds than females ($H_3$).

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection and processing

Wandering albatrosses on Possession Island, Crozet Islands (46°24′S; 51°46′E) and Bird Island, South Georgia (54°00′S, 38°03′W) were individually marked and sexed from field observations (size and plumage, copulatory position) or from genetic analyses. GPS loggers (IgotU 120/600 Mobile Action Technology©) were deployed on incubating albatrosses from Crozet in 2010–2016 ($n$ = 276) and from South Georgia in 2012 ($n$ = 42), and in 2016, X-GPS radar loggers were also deployed on birds at Crozet ($n$ = 47; see Weimerskirch, Filippi, Collet, Waugh, & Patrick, 2018 for details). IgotU devices were programmed to record a location (longitude and latitude) every 15 and 25 min, at Crozet and South Georgia, respectively, and X-GPS devices recorded locations at a much finer sampling rate (1 Hz). Devices were attached to the back feathers using Tesa© tape and left on birds for one or more foraging trips (Table S1 in Appendix S1).

All data processing and statistical analyses were conducted in R *v.* 3.5.2 (R Core Team 2019). We defined the start and end of each foraging trip as the last GPS fix at departure, and the first after arrival back at the colony, and filtered out unrealistic positions, that is, those that required an estimated flight speed above 90 km/hr, based on an iterative forward/backward averaging filter (McConnell, Chambers, & Fedak, 1992). As HMMs require regular time intervals but GPS devices take variable times to acquire satellites, the fixes were linearly interpolated to 15 and 25 min intervals for birds from Crozet and South Georgia, respectively, using the ADEHABITATLT package (Calenge, 2006).

### 2.2 | Wind data

We obtained hourly zonal (i.e. latitudinal, $V_u$) and meridional (i.e. longitudinal, $V_v$) wind speed components from the European Centre for Medium Range Weather Forecasts (ECMWF) ERA5 reanalysis dataset (Copernicus Climate Change Service (C3S), 2017). Data were available at a spatial resolution of 0.28°, corresponding to around a 15–30 km resolution given the latitudes used by the tracked birds. We selected winds at 10 m a.s.l. as this is similar to the mean observed flight height (8 m; Pennycuick, 1982). Wind data nearest in time to each tracking location were extracted using the RASTER package (Hijmans et al., 2019). We computed wind speed and direction at each location from zonal and meridional components and calculated flight direction relative to wind direction (hereafter relative wind direction), which was the absolute difference between the bearing of the bird and wind direction, scaled to between 0° (tailwind) and 180° (headwind) to remove directionality.

### 2.3 | Comparing wind conditions

We first assessed whether wind speeds experienced by birds varied by population and sex using linear mixed effects models (LMMs) in the LME4 package (Bates et al. 2015). Wind speed was modelled as the response variable with a Gaussian error distribution, and the factors population, sex, their two-way interaction

and year included as covariates. A random effect of trip identity nested within individual identity was included to account for variation in the number and duration of trips per individual respectively. We performed multi-model inference on the full set of predictor combinations and assessed the best-supported model as that with the lowest Akaike Information Criterion (AIC). As small differences in AIC are not considered to be meaningful (Burnham & Anderson, 2002), if multiple models were within two AIC units, the best model was deemed to be that which had the fewest number of parameters (i.e. the most parsimonious) (Harrison et al., 2018). Additionally, we compared wind directions experienced by sex and population using Watson's two-sample tests of homogeneity in the CIRCULAR package (Lund et al. 2017).

## 2.4 | Behavioural classification

We fitted three-state HMMs to the interpolated tracks within the MOMENTUHMM package (McClintock & Michelot, 2018) in order to: (a) identify states as proxies of discrete behaviours and (b) model the effect of covariates on the probability of transitioning between states (Grecian, Lane, Michelot, Wade, & Hamer, 2018; Patterson et al., 2009). We considered the three states using two input variables, step lengths and turning angles; directed flight (high speeds, shallow turning angles), ARS (moderate speeds, moderate to wide turning angles) and rest (low speeds, shallow to moderate turning angles). A gamma distribution was chosen for step lengths and a von Mises distribution for turning angles. We used the Viterbi algorithm to estimate the most likely sequence of behavioural states from the fitted model (Rabiner, 1989). HMMs require initial values of step and angle distributions to be specified for each state to facilitate parameter estimation, so to fix these values, we first chose them at random 100 times within a range of biologically realistic values, and then determined the most appropriate values as those closest to the most frequently estimated. HMMs were run separately for each population due to differences in the sampling resolution.

We used an expert-driven approach to assess if the model was assigning appropriate sequences of behaviours. Briefly, for a random selection of trips, we manually iterated through trajectories and classified states based on movement patterns. The performance of HMMs was then assessed by comparing model- and visually assigned behaviours at each step (see Appendix S2 for details). Immersion loggers (MK19; British Antarctic Survey, Cambridge), which recorded bouts of wet or dry at 6 s resolution, were also deployed on birds at South Georgia (Froy et al., 2015); these data were used to compare model-assigned behavioural bouts with finer scale activity sequences (Appendix S2).

## 2.5 | Modelling covariates on behavioural transition probabilities

We tested whether the probability of transitioning between states was influenced by sex and wind variables. To do so, we first removed complete trips or sections of trips over the shelf areas of Crozet and South Georgia (see Appendix S1 for details), representing regions where birds are frequently attracted to fishing vessels (Collet, Patrick, & Weimerskirch, 2015; Weimerskirch et al., 2018; Xavier et al., 2004). In these areas, changes in behaviour through attraction to vessels (Corbeau, Collet, Fontenille, & Weimerskirch, 2019) could weaken our ability to detect responses to environmental cues such as wind. While fishing vessels operate throughout other parts of their foraging range (e.g. off South America or southern Africa; Clay et al. 2019), the likelihood of encounter is substantially lower and so is less likely to influence our results (Corbeau et al., 2019; Weimerskirch et al., 2018). As foraging and flight behaviour of albatrosses varies by day and night (Phalan et al., 2007; Weimerskirch et al., 1997), for each GPS location we also assigned daylight (including civil twilight, when the sun is 6° below the horizon) or darkness using the R package MAPTOOLS (Bivand et al., 2020) and included this variable (hereafter LoD) in models to test for different responses to wind by day and night.

We ran a series of HMMs including all combinations of the covariates sex, wind speed, LoD, as well as the two-way interactions between wind speed and LoD, and wind speed and sex. For models which included wind speed, three further model combinations were run, including (a) the quadratic effect of wind speed to capture non-linear responses, (b) relative wind direction and (c) relative wind direction and its interaction with wind speed. We specified the transition matrix allowing covariates to influence transition probabilities between all states. In total, 40 models were run for each site and model selection was based on AIC. To check that best supported models were not over-parameterized, we also compared AIC with models for which covariate values had been reshuffled (see Appendix S3).

As models were run separately for South Georgia and Crozet, we assessed whether responses differed between populations by checking if parameters on the beta (i.e. working) scale (Patterson et al., 2017) and their 95% CIs overlapped. We also determined if transitions between individual states (e.g. ARS to rest) were significantly influenced by covariates based on whether these parameters and CIs overlapped zero. In order to visualize how covariates influenced overall time–activity budgets, we plotted stationary probability distributions, which represent the equilibrium of the Markov process (i.e. whether it changes as time progresses; Patterson et al., 2009). Lastly, to determine the sensitivity of our results to the selected flight height (10 m a.s.l.), we reduced wind speeds to reference heights of 5 and 2 m a.s.l., and carried out model selection as previously described (see Appendix S3 for details). Goodness of fit and autocorrelation were assessed by QQ, pseudo-residual and autocorrelation plots (Patterson et al., 2009; Pohle, Langrock, van Beest, & Schmidt, 2017). Unless otherwise specified, all means are presented ± *SD*.

# 3 | RESULTS

Wandering albatrosses were tracked for a total of 347 trips (176 male and 171 female) from Crozet and 38 trips (21 male and 17 female) from South Georgia (for details of sample sizes at Crozet by year, see

Appendix S1), and at both populations, females foraged further north than males (Figure 1; sensu Froy et al., 2015; Weimerskirch et al., 1993).

## 3.1 | Wind conditions experienced

Albatrosses from both populations experienced similarly large ranges of wind speeds (Crozet: 0.5–23.0 m/s; South Georgia: 0.1–23.6 m/s). The best model comparing wind speeds experienced retained the covariates sex, population, their two-way interaction and year (Table 1). Individuals from Crozet experienced marginally stronger winds on average than those at South Georgia (modelled mean difference ± 95% CI: 1.4 ± 0.7 m/s; Figure 2). While we found no sex difference for South Georgia birds, males at Crozet experienced greater wind speeds on average, than females (modelled mean difference ± 95% CI: 0.9 ± 0.5 m/s). Individuals predominantly experienced south-westerly winds (mean [lower–upper 95% CI] = 281° [277°–284°]) and we found no difference in the mean wind direction experienced between populations (Watson's two-sample test for homogeneity, $U^2 = 0.08$, $p > 0.10$). As with wind speeds, when split by population, there was a marginal, but significant, sex difference in average wind directions experienced at Crozet ($U^2 = 0.35$, $p < 0.01$) but no difference at South Georgia ($U^2 = 0.12$, $p > 0.10$).

## 3.2 | Behavioural classification

Both males and females spent roughly a third of their time on foraging trips in each of the three states: directed flight, ARS and resting on the sea surface (Table 2). Distributions of step lengths and turning angles for each state were very similar between populations, indicating

**TABLE 1** Generalized linear mixed models comparing wind speeds experienced by foraging wandering albatrosses *Diomedea exulans* from Crozet and South Georgia. (a) Selection of the top five best supported models; the most parsimonious is in bold and (b) its parameter estimates (± *SE*). X: predictor variables retained and –: not retained, in the most parsimonious models; ΔAICc: change in Akaike information criterion, corrected for small sample sizes, from the best-supported model

(a)

| Covariates | | | | | | |
|---|---|---|---|---|---|---|
| Year | Sex | Population | Population: Sex | *df* | AICc | ΔAICc |
| **X** | **X** | **X** | **X** | **13** | **2,036,088** | **0.0** |
| X | X | X | – | 12 | 2,036,093 | 4.6 |
| X | X | – | – | 11 | 2,036,109 | 20.7 |
| X | – | X | – | 11 | 2,036,116 | 27.8 |
| X | – | – | – | 10 | 2,036,130 | 41.5 |

(b)

| Parameter | Estimate |
|---|---|
| Intercept (Crozet, female, 2010) | 8.37 ± 0.41 |
| Sex (male) | −0.80 ± 0.43 |
| Population (South Georgia) | 0.90 ± 0.15 |
| Population (South Georgia):Sex (male) | −1.19 ± 0.47 |
| Year (2011) | −1.08 ± 0.46 |
| Year (2012) | 1.38 ± 0.48 |
| Year (2013) | 0.26 ± 0.43 |
| Year (2014) | 0.21 ± 0.51 |
| Year (2015) | −0.46 ± 0.54 |
| Year (2016) | 0.14 ± 0.43 |

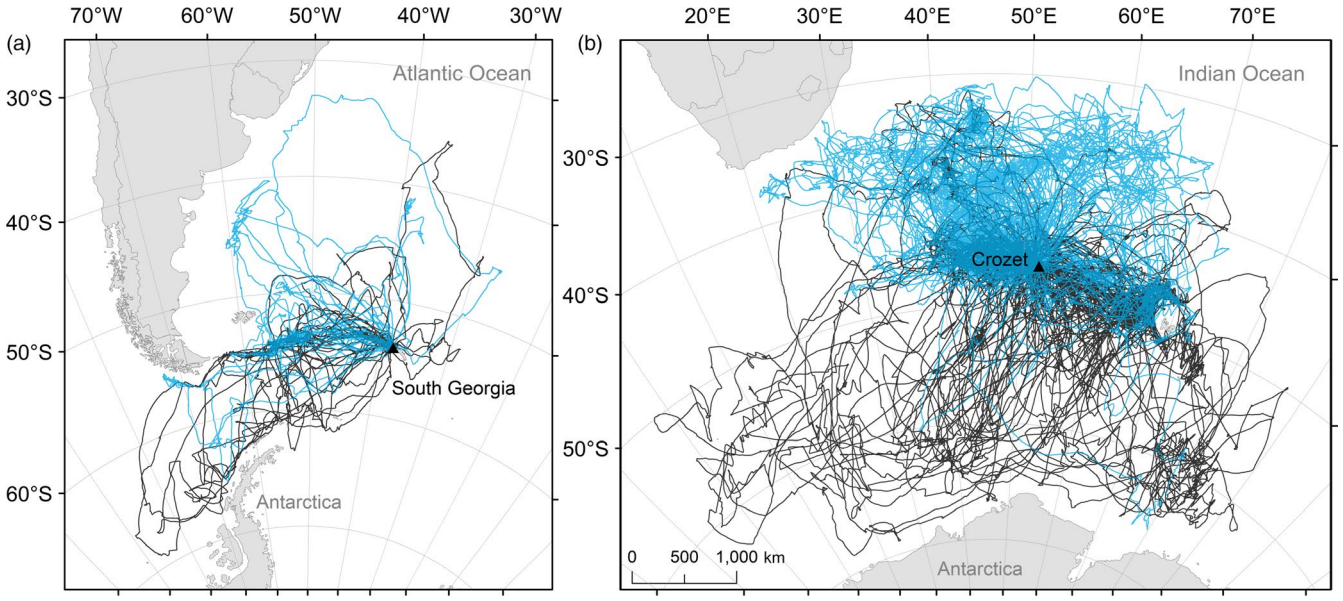



**FIGURE 1** Foraging trips of female (blue) and male (black) wandering albatrosses *Diomedea exulans* tracked with GPS loggers during incubation from (a) South Georgia and (b) Crozet. The colony locations are shown by black triangles and both maps are shown in the Azimuthal Equal Area projection centred on the colony

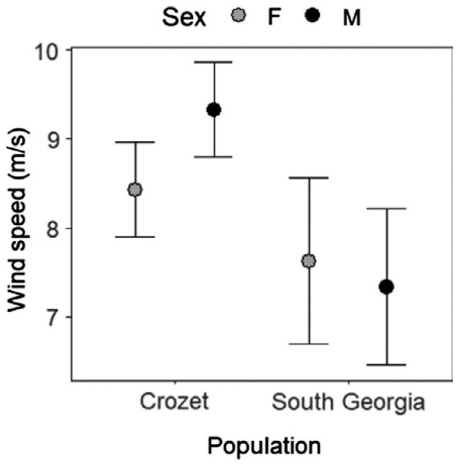
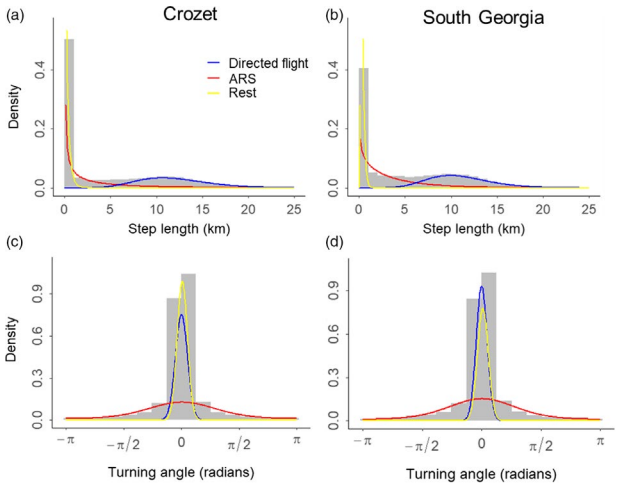



**FIGURE 2** Wind speeds (at 10 m a.s.l.) experienced by foraging wandering albatrosses *Diomedea exulans* tracked during incubation with GPS loggers from Crozet and South Georgia. Points are modelled means ± 95% confidence intervals from generalized linear mixed models comparing wind speeds experienced by sex and population




(e)

| State at time $t$ | State at time $t+1$: Directed flight | ARS | Rest |
|---|---|---|---|
| Directed flight | 0.880 | 0.120 | <0.001 |
| ARS | 0.155 | 0.790 | 0.056 |
| Rest | <0.001 | 0.139 | 0.861 |

(f)

| State at time $t$ | State at time $t+1$: Directed flight | ARS | Rest |
|---|---|---|---|
| Directed flight | 0.870 | 0.130 | <0.001 |
| ARS | 0.159 | 0.765 | 0.076 |
| Rest | <0.001 | 0.212 | 0.788 |

**FIGURE 3** Histograms of observed step lengths (a, b) and turning angles (c, d) for Crozet (left column) and South Georgia (right panel). Lines represent HMM-fitted state distributions coloured according to the state: directed flight, area-restricted search (ARS) and rest. The GPS sampling resolution of the two populations was different, but for plotting purposes, step lengths for South Georgia have been transformed so they match Crozet (15 min resolution). (e–f) Transition probability matrix for the final three-state (e) Crozet and (f) South Georgia HMMs. For a given state at time $t$, the matrix shows the probabilities of transitioning to each of the other states, or remaining in the same state at time $t + 1$

**TABLE 2** The percentage of time spent in each of the three behavioural states (directed flight, area-restricted search and rest) on foraging trips for male and female wandering albatrosses *Diomedea exulans* from the Crozet Islands and South Georgia. Values are mean percentages ± *SD* for each group

| | Crozet | | South Georgia | |
|---|---|---|---|---|
| | Male | Female | Male | Female |
| Directed flight | 27.6 ± 17.2 | 32.4 ± 15.7 | 33.4 ± 10.3 | 34.6 ± 8.6 |
| ARS | 36.0 ± 13.0 | 34.9 ± 12.9 | 35.2 ± 7.1 | 39.5 ± 5.8 |
| Rest | 36.4 ± 16.0 | 32.6 ± 14.1 | 31.3 ± 7.8 | 25.9 ± 7.8 |

similar behaviour by both sets of birds (Figure 3a–d). The probability of transitioning between or remaining in states was also similar; a high probability (at least 0.75) of remaining in each state indicated that behavioural bouts generally lasted longer than the GPS sampling interval (Figure 3e–f). However, inspection of transition matrices revealed that the probability of transitioning from rest to directed flight was negligible (Figure 3e–f; Figures S5 and S6 in Appendix S3); instead, the model often classified an intermediate ARS location, probably because the GPS sampling resolution could not capture the precise timings of take-offs or landings (Figure S2 in Appendix S3). When comparing outputs of HMMs to finer scale immersion data for birds at South Georgia, there was a good match for directed flight and rest, but during ARS, birds undertook finer scale sequences of wet and dry activity likely associated with prey capture attempts, which were not apparent from the lower frequency GPS fixes (Table S3 in Appendix S2).

## 3.3 | Effects of covariates on transition probabilities

For both populations, behavioural responses varied according to wind speed and relative direction, and sex, as indicated by their three-way interaction (Table S4 in Appendix S3). The best-supported models had overwhelming support (ΔAIC of 408.3 and 16.8 compared to next best models for Crozet and South Georgia, respectively; Table S4). Although models were run separately for each population, there was little evidence of divergent responses to wind between the two populations, based on substantial overlap in model coefficients (beta parameters) and their CIs (Table S5; Figure S3 in Appendix S3). For both populations, models were robust to the selection of flight height (Appendix S3).

### 3.3.1 | Effect of winds on movement decisions

Wind speed influenced the likelihood of switching between all behavioural states based on the estimated CIs (Table S5; Figure S3). Transition probabilities generally increased with increasing wind speed, except for ARS to rest (i.e. landing), directed flight to ARS for Crozet birds and ARS to directed flight for South Georgia birds, for which the probability decreased (Figure 4; Figure S5). Relative wind direction (i.e. from tailwind to headwind) followed a similar pattern to wind speed; in headwinds, birds were more likely to transition

from directed flight to ARS and less likely to land (Figure 4; Figure S5). However, while there was only slight variation in transition probabilities with respect to wind speed and relative direction for most state transitions (i.e. probability difference of *c*. 0.1–0.2 for range of wind values), the effect of both wind speed and relative direction on the transition from rest to ARS (i.e. taking-off) was much more pronounced (i.e. probability difference of *c*. 0.1–0.6). Birds were much more likely to take off in stronger winds and in crosswinds to headwinds, with probabilities increasing substantially in winds above 10 m/s (Figure 4; Figure S6).

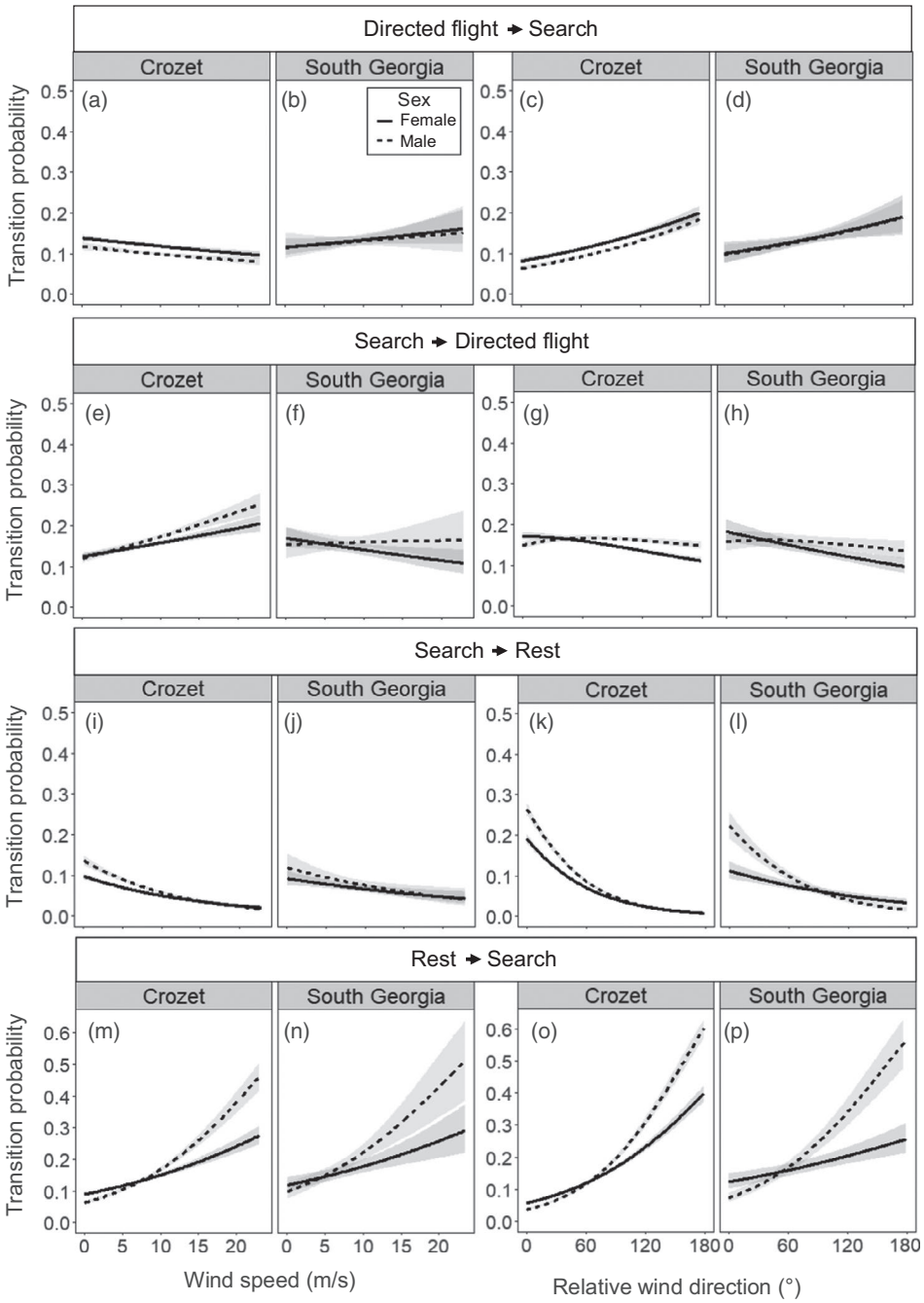



**FIGURE 4** Model-estimated transition probabilities in relation to wind speed (a–b, e–f, i–j, m–n; at 10 m a.s.l.) and wind direction relative to bird trajectories (c–d, g–h, k–l, o–p) derived from hidden Markov models for foraging male and female wandering albatrosses *Diomedea exulans* from Crozet and South Georgia during daylight hours. The major behavioural transitions shown are as follows: directed flight to area-restricted search (a–d), search to directed flight (e–h), search to rest (i–l) and rest to search (m–p). As the probability of transitioning from directed flight to rest and vice versa was zero, we consider the transition from rest to search to represent taking-off behaviour, and from search to rest, landing on the sea surface. Model-estimated coefficients are shown as black lines for females (continuous) and males (dashed) with 95% confidence intervals as grey shading. Note that the *y*-axis extents differ

### 3.3.2 | Sex differences in responses to winds

Sex differences in responses to wind were similar for both populations (Table S5; Figure S3). In low wind speeds (<5 m/s) the probability of taking-off was slightly higher for females than males (Table 3; Figure 4). This pattern was reversed as wind speeds increased, with a higher probability of take-off for males than females in moderate to high wind speeds (>5 m/s). Notably, in wind speeds >20 m/s, males were much more likely to take off than females, by a probability of *c*. 0.20 (Figure 4). In addition, males were more likely to transition from ARS to directed flight in stronger winds and much more likely to land in weaker tailwinds. Between populations, model-estimated effects of winds were similar (Table S5; Figure S3); however, the probability of transitioning from directed flight to ARS increased slightly with increasing wind speed for birds from South Georgia, but decreased slightly for those from Crozet (both by a probability of *c*. 0.03 from 0 to 20 m/s; Figure 4).

### 3.3.3 | Time–activity budgets

Time–activity budgets with respect to the covariates were calculated from stationary probability distributions (Figure 5). For mean values of wind, males were more likely to be in directed flight and less likely to be in ARS than females, with greater sex differences at Crozet. With increasing wind speeds and relative wind direction, birds were more likely to be in directed flight or ARS, than rest (Figure 5). Increases in the probability of directed flight appeared

**TABLE 3** Sex differences in the predicted probability of transitioning from rest to area-restricted search, representing take-off behaviour, at different wind speeds. Predictions are derived from hidden Markov models for foraging male and female wandering albatrosses *Diomedea exulans* from Crozet and South Georgia during daylight hours. Wind speeds have been averaged over 5 m/s intervals encompassing wind speeds encountered (wind speeds at 5–10 and 10–15 m/s representing moderate and high wind speeds, respectively, have been pooled as sex differences were similar), and 95% confidence intervals provided in parentheses

| | Crozet | | South Georgia | |
|---|---|---|---|---|
| **Wind speed** | **Females** | **Males** | **Females** | **Males** |
| Low (<5 m/s) | 0.10 (0.10–0.11) | 0.08 (0.07–0.09) | 0.13 (0.11–0.15) | 0.12 (0.10–0.15) |
| Moderate–high (5–15 m/s) | 0.15 (0.14–0.16) | 0.17 (0.16–0.18) | 0.18 (0.16–0.20) | 0.22 (0.20–0.26) |
| Very high (>15 m/s) | 0.23 (0.21–0.25) | 0.36 (0.33–0.39) | 0.25 (0.20–0.31) | 0.41 (0.3–0.51) |

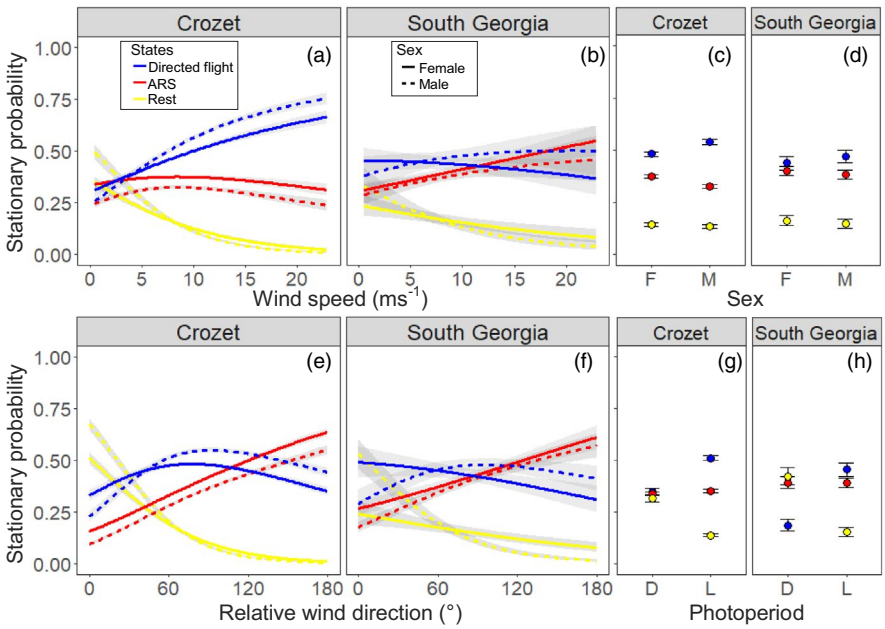



**FIGURE 5** Time–activity budgets in relation to covariates. Hidden Markov model (HMM)-estimated stationary probabilities of being in each of the three states (blue = directed flight; red = area-restricted search [ARS]; yellow = rest) for given values of wind speed (a–b; at 10 m a.s.l.), sex (c–d; F = females, M = males), relative wind direction (e–f) and photoperiod (g–h; D = darkness, L = daylight), for foraging wandering albatrosses *Diomedea exulans* from Crozet and South Georgia. As the two-way interactions between sex, and wind speed and direction, were retained in best supported HMMs, probability distributions are shown as separate lines for females (continuous) and males (dashed) in a–b and e–f. All plots are shown either with 95% confidence intervals as shaded polygons or error bars. Note that the stationary distribution represents the equilibrium of the process (i.e. it remains unchanged as time progresses)

to be driven more by increasing wind speeds (from 0 to 20 m/s by 0.47 and 0.32 for Crozet males and females and by 0.12 and 0.07 for South Georgia males and females), and of ARS by increasing orientation into headwinds (from 0° to 180° by 0.46 and 0.48 for Crozet males and females and by 0.39 and 0.34 for South Georgia males and females). The latter suggests that directed flight and ARS are favoured in tail- and headwinds respectively. Behaviour also varied by day and night; as expected, birds were more likely to rest during darkness than daylight; however, a substantial amount of ARS behaviour (stationary probability of *c*. 0.25) still took place during darkness (Figure 5).

## 4 | DISCUSSION

Our study provides strong evidence that wandering albatrosses adjust their foraging behaviour according to variation in wind conditions. We found that flight decisions of foraging birds, particularly the decision to take off from rest to flight, were influenced by wind speed and relative direction, and were remarkably similar between populations, indicating a shared, likely morphological, constraint on flight. Moreover, while the sexes responded to wind in a broadly similar manner, the response was markedly stronger in males, which were much more likely than females to take off in stronger winds (by *c*. 20% in wind speeds >20 m/s). Owing to their different foraging distributions, resulting in variation in wind speeds and directions experienced, as well as variation in responses to those conditions, overall time–activity budgets differed between males and females. Thus, our results confirm that wind strongly influences sex-related foraging behaviours (Phillips et al., 2004; Shaffer et al., 2001) with wider implications for population dynamics (Weimerskirch, 2018).

### 4.1 | Wind effects on movement decisions and time–activity budgets

Many species of soaring seabirds are known to conduct looping trips which take advantage of ocean basin-scale wind circulation patterns (e.g. Adams & Flora, 2009; Clay, Oppel et al., 2019; Weimerskirch et al., 2000), yet foraging decisions at the scale of hours to days are thought to predominantly be linked to the distribution of prey (Pinaud & Weimerskirch, 2005; Weimerskirch et al., 2005). We show that over the course of a foraging trip, birds adjust their behaviour according to variation in wind encountered. Moreover, the effect of wind on behavioural responses (as determined by the slope of the relationship) was most pronounced for behaviours which are known to be the energetically expensive, that is, taking-off, indicating that birds seem to pursue an energy-saving strategy, modulating their behaviour to reduce unnecessary flight costs where possible (Shepard et al., 2013).

Due to their long wings, soaring birds such as albatrosses produce low thrust at slow speeds (Alerstam et al., 1993) and so the muscular effort associated with take-off is particularly costly (Bevan, Butler, Woakes, & Prince, 1995; Duriez et al., 2014; Weimerskirch et al., 2000). As predicted ($H_1$), the probability of take-off increased in stronger winds, and in relatively windless conditions, birds were more likely to spend time resting on the sea surface. Prey is often captured just after landing, after which birds can spend long periods on the sea surface, thought to be related to prey handling or digestion, sleep or rest (Weimerskirch et al., 1997). As the probability of resting was substantially reduced in moderate to strong winds, our results support previous suggestions that birds have flexible sleep, rest and digestion requirements (Phalan et al., 2007), and that extensive periods on the water may be indicative of light winds that prevent flapping flight. Indeed, anecdotal evidence suggests that albatrosses remain 'grounded' in windless high pressure zones for several days, particularly in subtropical regions, where they might be at risk of starvation (Jouventin & Weimerskirch, 1990).

Our analysis also revealed that birds were more likely to transition from rest to flight into headwinds. Aerodynamic theory predicts that birds should take off into the wind, as they would commence with an airspeed equal to the wind speed, reducing the effort required to accelerate to the minimum power speed (the flight speed which requires the lowest energy to maintain flight; Pennycuick, 2008). Indeed, this has also been recently demonstrated in the pursuit-diving European shag *Phalacrocorax aristotelis* (Kogure, Sato, Watanuki, Wanless, & Daunt, 2016). As far as we are aware, this has not been previously shown in a soaring seabird; yet, due to the relatively coarse resolution of our analysis, future studies using higher resolution wind and behavioural data are needed to confirm this observation (see below).

As wind speeds increased beyond the minimum threshold for dynamic soaring (3–4 m/s; Sachs, 2005), there was an increased likelihood that birds would be in directed flight rather than ARS in stronger winds, which supported our second prediction ($H_2$). This is in line with theoretical expectations that birds should fly at lower speeds, closer to the minimum power speed when searching for prey, to facilitate prey detection and handling (Hedenström & Alerstam, 1995; Richardson, Phillips, & Wakefield, 2018). Following odour plumes is probably more challenging in strong winds, as is visual detection of prey due to higher swells and rippling to the sea surface (Dunn, 1973; Nevitt, Losekoot, & Weimerskirch, 2008). As wind speeds increased, the probability of transitioning from ARS to directed flight increased for Crozet birds, but the opposite pattern was found at South Georgia; the reason for this is unclear, but may be related to different availability of winds or prey between the two regions (Phillips, Wakefield, Croxall, Fukuda, & Higuchi, 2009). Nonetheless, for both populations there was a greater probability of search behaviour in headwinds than tailwinds indicating that birds preferentially orient into winds, likely using olfaction to localize prey (Nevitt et al., 2008).

### 4.2 | Sex differences in responses to winds

In support of our third prediction ($H_3$), we found the decisions of males were more strongly influenced by wind than females; in

particular, males were much more likely to take off in strong headwinds. In albatrosses and giant petrels *Macronectes* spp., males can be larger by 20% or more, and have higher wing loading (González-Solís et al., 2000; Phillips et al., 2004; Shaffer et al., 2001). As a result, males have a higher minimum power speed (i.e. greater power required for take-off), so are predicted to be more reliant on wind for uplift (Shaffer et al., 2001). Indeed, differences between the sexes were most pronounced for take-off, with males less likely to do so in windless conditions, indicating a constraint on energetic flapping flight (Bevan et al., 1995; Weimerskirch et al., 2000). In contrast, sex differences in transitions between other behaviours, such as from directed flight to ARS or vice versa, were slight, implying that when in flight, males and females respond to wind more subtly, likely through changes to air speeds (Richardson et al., 2018; Wakefield et al., 2009).

While this is the first study to examine behavioural-state changes in response to wind in a soaring seabird, in a recent study of sexually dimorphic Andean condors *Vultur gryphus*, larger males scheduled their daily routines to align more closely with the availability of thermal uplift than smaller females (Alarcón et al., 2017). In contrast, for griffin vultures *Gyps fulvus*, which are monomorphic, flight decisions did not differ between the sexes (Harel et al., 2016). Thus, it appears that sex-specific flight behaviour in soaring birds is well-explained by morphological differences, rather than other factors, such as reproductive constraints (Phillips et al., 2004; Shaffer et al., 2001). While male wandering albatrosses are on average larger and have higher wing loading than females (Shaffer et al., 2001), there is a small degree of overlap, such that if wing loading was the predominant factor explaining differential foraging distributions and flight responses, smaller males should be more similar in behaviour to larger females than larger males. Future studies which link individual body and wing characteristics of males and females with wind use might further disentangle the roles of sex and size on flight behaviour.

Responses of birds from both populations to winds (using two independent models) were very similar, despite large differences in sample size and regional differences in wind fields and in other environmental characteristics related to prey abundance and distribution (Phillips et al., 2009), indicating shared morphological constraints on flight. At low wind speeds (<5 m/s) males from both populations were less likely to take off than females; this indicates that it may be more energetically challenging for them to routinely forage in areas with persistently low wind speeds. Indeed, it has been proposed that flight performance explains the more southerly distribution of males in regions with more persistent low pressure cells and their associated stronger wind speeds (Shaffer et al., 2001). While it was not our aim to examine the proximate drivers of sexual segregation, that males and females from South Georgia experience broadly similar wind speeds (Wakefield et al., 2009) suggests that flight performance is only one of several non-exclusive factors, such as size-mediated competitive exclusion, explaining sexual segregation (Phillips et al., 2004; Weimerskirch et al., 1993). Indeed, the reduced geographic area over which to forage in the southwest Atlantic Ocean compared to the southwest Indian Ocean, and reduced variability in wind fields, likely lead to the more nuanced patterns of sexual segregation (see also Wakefield et al., 2009).

### 4.3 | Model limitations

State classifications were remarkably similar between the two populations suggesting that the models were biologically meaningful, however, we acknowledge that due to the GPS sampling resolution, we could not resolve behaviour at finer scales. Moreover, global circulation models are designed to represent an averaged state of the atmosphere and currently do not resolve wind patterns on micro- and mesoscale levels, for example, from turbulence and gusts (Shamoun-Baranes et al., 2017). As biases were similar across groups (sex and population) and as major transitions between resting and flight (either directed flight or ARS) were still detected, these factors should not have material effects on our results. When we compared HMM-assigned states to finer scale immersion activity for South Georgia birds, the two datasets accorded well for directed flight and rest, but during ARS flight we were not able to capture sequences of take-offs and landings, likely associated with prey capture (Weimerskirch et al., 1997). We note that birds expend substantial energy locating and capturing prey (e.g. Amélineau et al., 2014), behaviours which are presumably influenced to a lesser degree by variation in modelled wind averaged at the resolution of interest (hourly). Hence, studies which complement GPS loggers with other sensors such as immersion loggers or accelerometers, as well as barometric pressure sensors and anemometers, should provide a better understanding of flight responses to in situ variation in the atmosphere (Williams et al., 2020). Lastly, we were unable to measure flight heights of the tracked birds. Wind speed varies with altitude, and while models run using wind values at 2, 5 and 10 m a.s.l. were similar, we acknowledge that wind speeds will vary according to behavioural state (and associated flight height) and may differ from those reported here. As this bias is similar across sexes and populations, it is unlikely to detract from our main conclusions.

## 5 | CONCLUSIONS

We have demonstrated in a soaring seabird that behaviour is adjusted flexibly to wind conditions, and that due to differences in flight morphology, males were more likely to modulate flight decisions to wind than females. Their reliance on stronger winds for energy-efficient flight may also explain the preference of males for windier habitats (Shaffer et al., 2001), at least at Crozet, where the greater availability of oceanic habitat promotes segregation between the sexes. While we did not predict how time–activity budgets would change under future wind scenarios, the greater proportion of time spent in flight in strong winds supports empirical evidence that over recent decades foraging albatrosses in the Indian Ocean have increased

travel speeds and reduced time spent on the water in response to increases in average wind speeds (Weimerskirch et al., 2012). Given that global circulation patterns are changing as a result of climate change (Young, Zieger, & Babanin, 2011), a greater understanding of the mechanistic links between wind, movements and energetics is crucial for predicting how seabird populations may respond in the future (Lewis, Phillips, Burthe, Wanless, & Daunt, 2015; Thorne et al., 2016; Weimerskirch et al., 2012).

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## AUTHORS' CONTRIBUTIONS

T.A.C., S.C.P. and R.J. conceived the ideas and designed the methodology; H.W. and R.A.P. oversaw tracking data collection and T.A.C. and O.d.O. acquired wind data; T.A.C. processed and analysed the data with assistance from R.J.; T.A.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

GPS data can be downloaded from the BirdLife International Seabird Tracking Database (http://seabirdtracking.org/mapper/; dataset ids: 1133, 1134, 1135, 1136, 1137, 1138, 1503). The datasets and R codes to run analyses and reproduce Figures 2, 4 and 5, are freely available on Zenodo https://doi.org/10.5281/zenodo.3824064 (Clay et al., 2020). The ECMWF ERA5 data are available through the Copernicus Climate Change Service Climate Data Store (https://cds.climate.copernicus.eu/#!/home).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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