Remotely-sensed wind speed predicts soaring behaviour in a wide-ranging pelagic seabird

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Abstract

Global wind patterns affect flight strategies in many birds, including pelagic seabirds, many of which use wind-powered soaring to reduce energy costs during at-sea foraging trips and migration. Such long-distance movement patterns are underpinned by local interactions between wind conditions and flight behaviour, but these fine-scale relationships are far less well-understood. Here we show that remotely-sensed ocean wind speed and direction are highly significant predictors of soaring behaviour in a migratory pelagic seabird, the Manx shearwater (*Puffinus puffinus*). We used high-frequency GPS tracking data (10Hz) and statistical behaviour state classification to identify two energetic modes in at-sea flight, corresponding to flap-like and soar-like flight. We show that soaring is significantly more likely to occur in tailwinds and crosswinds above a wind speed threshold of around 8ms^{-1}, suggesting that these conditions enable birds to reduce metabolic costs by preferentially soaring over flapping. Our results suggest a behavioural mechanism by which wind conditions may shape foraging and migration ecology in pelagic seabirds, and thus indicate that ~~climate change-driven~~ shifts in wind patterns ~~shifts~~ driven by climate change could impact this and other species. They also emphasise the emerging potential of high-frequency GPS biologgers to provide detailed quantitative insights into fine-scale flight behaviour in free-living animals.

Keywords: movement ecology, seabirds, tracking, remote sensing, wind, soaring

1. Introduction

The effects of global-scale environmental variables (e.g. temperature, precipitation) on animal ecology are well-known, but similar relationships with wind have been much less extensively studied. Wind conditions affect phenology, migration routes, ecological interactions and foraging success in many volant animals including birds, bats and insects (e.g. [1–4]). Recent GPS tracking studies have shown that global winds affect long-distance patterns of foraging and migration behaviour in various wide-ranging bird species [5–8], however much less is known about the effect of more localised wind conditions. Understanding such fine-scale interactions between flight behaviour and the environment is key to understanding how individual behavioural responses to wind scale up to shape movement patterns at large spatial scales and over evolutionary time, such as the evolution of stable migration routes [8,9]. In a conservation context, such knowledge is also important to predict how shifts in atmospheric conditions under climate change [10–12] may impact many migratory birds.

Pelagic seabirds are top marine predators that regularly travel hundreds ~~or thousands~~ of kilometres during foraging and migration [13], making them particularly reliant on ocean wind patterns [14–17]. During these journeys many albatrosses and shearwaters (Procellariiformes) engage in specialised modes of wind-powered soaring behaviour, thought to be metabolically less ~~metabolically~~ costly than flapping flight [18–20]. Data from GPS and accelerometer tags are now providing insights into soaring in free-living albatrosses and other birds [21–23], however much remains unknown about the fine-scale relationship between local winds and soaring behaviour. In this study we use very high-frequency GPS tracking (10Hz) to show that wind speed and direction, measured via satellite remote sensing, are highly significant predictors of soaring behaviour in a migratory pelagic seabird, the Manx shearwater (*Puffinus puffinus*). Manx

shearwaters are small (~400g), burrow nesting, pelagic seabirds. They are Amber listed in the UK [24] where most (~80%) of the global Manx shearwater population nests. They forage from breeding colonies around the UK coastline each summer before migrating to overwinter off southern Argentina, making an annual round trip of over 20,000km [9, 25–27].

We tracked breeding adults during at-sea foraging trips using custom GPS loggers that record bursts of 3D location fixes at 10Hz, and distinguished flight behaviour from each burst's mechanical energy characteristics. A bird's total mechanical energy at any time consists of the two components *kinetic* (related to speed) and *gravitational potential* energy (related to altitude). During flight, total energy can increase either through flapping, when stored chemical energy is converted to power in the wing muscles, or through input from an external energy source, e.g. wind [28]. Relative changes to the kinetic and potential energy components are determined both by the magnitude of energy input and the bird's current mode of movement. Different flight behaviours therefore show markedly different patterns of mechanical energy change over time, which can be calculated from high-frequency 3D GPS positional data (e.g. [22]). During soaring, tracked albatrosses show large cyclical variations in both potential (derived from altitude) and kinetic energy (derived from ground speed) as they ascend and descend through the shear wind gradient above the sea surface [22]. Although Manx shearwaters are 'flap-gliders', mixing intermittent wingbeat pulses with gliding and soaring [13], we hypothesised that wind-powered soaring in this species would show similar variations in energy and ground speed.

We therefore aimed to assess the prevalence of wind-powered soaring in Manx shearwaters and how this may vary under different environmental conditions. If, as might be expected, wind conditions play a role in how frequently soaring can occur, and soaring represents an energetically favourable mode of flight, then this has implications for the cost of movement

during travel and foraging. This can have knock-on effects upon how much effort is expended during reproduction, which has been demonstrated to impact breeding success in subsequent years [29]. Furthermore, quantifying the impacts of environmental conditions on the energetics of movement has potential implications for understanding the timing and success of migration and stopover [9]. This study also represents a proof of concept, demonstrating the potential of high-frequency GPS to analyse predictive relationships between movement and environmental conditions, with implications for understanding distribution, space-use and conservation of seabird species.

2. Methods

2.1. GPS tracking procedure

We tracked breeding adult birds during the chick-rearing season, between 12th and 25th August 2012 at the study colony on Lundy Island, Devon, UK (51.1781° N, 4.6673° W). We deployed our own custom GPS loggers (mataki.org [30]) on 8 birds. Devices were positioned on the back above the bird's centre of gravity and attached to feathers with marine tape, ensuring that if loggers could not be retrieved they would loosen and fall off within 2-3 weeks (see details in [25,31]). Study individuals weighed between 415 and 470g, and complete mass of devices including tape was less than 17g, under 3.6% of body mass. To maximise the proportion of foraging trips recorded, devices were programmed to record 10Hz bursts of GPS fixes for ~~up to~~ 60 seconds, at 30 minute intervals. Each fix recorded latitude, longitude and altitude, so each discrete sequence of 10Hz fixes (hereafter '*burst*') forms a detailed track of the bird's movement through its environment. All loggers were retrieved from recaptured birds and data were downloaded for analysis. One bird remained in its burrow for the study duration, so at-sea GPS

tracks were obtained from 7 birds (Table 1). ~~These birds recorded 7~~Seven complete foraging trips were recorded from these birds, with durations of 17.1 to 53.5hrs (mean 44.9 ± 23.8hrs), and 4 incomplete foraging trips during which the device battery expired before the bird returned to the colony.

ID	Number of bursts	Body mass before tracking (g)	Tracking time (hr)	Total distance (km)	Flap-like %	Soar-like %	Sitting %	Colony %	Wind speed (mean±sd) (ms^{-1})
1	114	445	79	625.1	21.9	26.3	35.1	16.7	11.05 ± 1.6
2	115	430	85.8	483.7	11.3	9.6	72.2	6.9	6.54 ± 3.59
3	56	440	46.8	282.6	17.8	25.0	51.8	5.3	10.97 ± 2.52
4	33	470	25.9	200.8	21.2	9.1	48.5	21.2	1.9 ± 0.25
5	44	465	28.5	123.1	22.7	4.5	43.2	29.5	7.09 ± 0.15
6	101	450	94.9	700.8	26.7	2.9	58.4	11.9	4.82 ± 3.0
7	96	440	76.9	462.8	8.3	31.3	37.5	22.9	10.58 ± 1.76

Table 1: Summary tracking statistics for all 7 birds, including proportion of recorded bursts classified as soar-like, flap-like, sitting and colony-associated, and average wind speed (mean ± sd) encountered during the tracking period.

2.2. Track processing and movement analysis

All analyses were carried out in R v. 3.1.2 [32]. Complete GPS tracks were filtered to exclude fixes with erroneous timestamps and those derived using fewer than four satellites, the minimum required for a precise three-dimensional location and time fix [25]. Each bird's track was split into its constituent bursts and ~~each burst's~~ the median latitude and longitude of each burst were assigned as its location. Since this study concerns at-sea activity, colony-associated bursts (within 1500m radius around Lundy, n=84) were excluded, as were information-poor bursts of fewer than 20 points (n=35), leaving a total of n=475 at-sea bursts. Within each burst we calculated distance and ground speed (velocity with respect to Earth's surface) between

successive fixes. Fixes with speeds exceeding 40 ms^{-1} were excluded as likely GPS errors [25]. To reduce the effect of any small GPS positional errors or missed fixes, we smoothed ground speed and altitude along each burst by applying a 15-point (1.5sec) rolling mean.

Following [23], from each fix's ground speed and altitude we calculated mechanical energy components kinetic (E_K), gravitational potential (E_P) and total energy ($E_T = E_K + E_P$), and also mechanical power (P), which measures the rate of E_T change across each between-fix time interval. These describe a bird's in-flight mechanical energy relative to the earth's surface (as inertial frame of reference), and their relative changes across a 60-second tracked burst describe flight dynamics in detail [22]. Although not directly related to metabolic energy expenditure, power values in excess of 0 indicate a net increase in mechanical energy over time, which could either be due to metabolic energy input (from wing muscles) or from the wind [28]. There is an upper limit to the power a bird can generate by flapping, therefore high power values and very large variation in E_K and power are strongly suggestive of wind energy input [22]. Further detail on track processing is provided in supplementary material (S1).

Tracking data are inherently statistically non-independent, with an animal's movement at any time being influenced by its recent activities, internal state and environment [33,34]. However, between-burst time intervals were sufficiently large (minimum 31.08min) to allow each to be treated as functionally independent. We therefore compared bursts by calculating the following summary parameters for each burst: (i) beeline distance (straight-line distance between burst start and end points); (ii) mean ground speed ('*mean speed*'); (iii) standard deviation of kinetic energy ('E_K *variance*'); (iv) standard deviation of power ('*power variance*'); and (v) straightness index (beeline distance divided by total path length), a measure of path tortuosity ranging from completely straight (SI=1) to randomly oriented (SI=0) [35].

Clusters in the distribution of summary parameters corresponding to putative flight modes were identified by fitting multivariate Gaussian mixture models (GMMs) by expectation-maximisation (EM), using mclust v.4.4 [36,37]. GMMs estimate the probability of each observation belonging to each cluster, and as such are a useful framework for identifying energetic modes from 60-second bursts of tracked flight, which often contain mixtures of flap-powered and wind-powered flight rather than single discrete behaviours. All variables were transformed to have mean 0 and standard deviation 1 before model fitting.

2.3. Modelling behavioural responses to environment

Metop/ASCAT remotely-sensed wind data (24-hour averaged at 0.25° resolution) were obtained from CERSAT (http://www.ifremer.fr/cersat). For each burst location this provided both total wind speed and separate zonal and meridional components, from which we calculated wind direction. Each burst's flight direction relative to wind ('*flight direction*') was calculated as the difference between burst beeline bearing and wind direction, and categorised as 'tailwind' (a difference of 0° to 50°), 'crosswind' (50° to 130°) or 'headwind' (130° to 180°), following [13]. We also obtained remotely-sensed data for sea surface chlorophyll *a* concentration (CHL), net primary productivity (NPP) and sea surface temperature (SST), to test possible relationships between flight mode and ocean productivity as proxy for prey abundance (see supplementary material S2). CHL and SST from Aqua and Terra MODIS were obtained from NASA OceanColor (4km, 8640 x 4320, 8-day composite, http://oceancolor.gsfc.nasa.gov/cms/). Aqua and Terra values were averaged where both were available, and missing data values were removed. Modelled NPP was obtained from Oregon State University Ocean Productivity (2160 x 4320, 8-day composite, http://www.science.oregonstate.edu/ocean.productivity/). We modelled

relationships between flight mode, wind and ocean productivity using logistic mixed-effects regression (lme4 v.1.1-7 [38]).

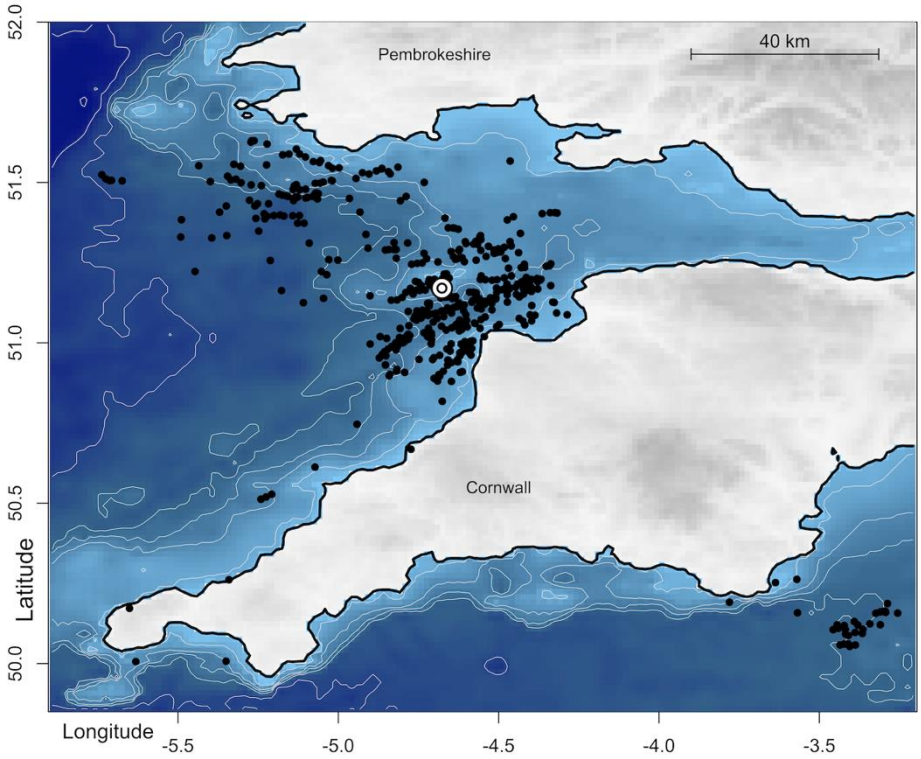

Figure 1: Distribution of Manx shearwaters foraging around Lundy Island (white circle), tracked between 12th and 25th August 2012 (n=7). Black points denote 60-second bursts of tracked movement (n=475) and are shown relative to the underlying bathymetry, accessed from National Oceanic and Atmospheric Administration (NOAA) via marmap [39].

3. Results

3.1. Flight mode classification

Foraging was mostly concentrated locally around Lundy and northwest towards Wales (Figure 1; mean distance from colony 33.0 ± 35.4km). Track processing yielded a final dataset of at-sea 10Hz bursts (n=475) (Figure 2; for more examples see supplementary material S4). Although most recorded for a full 60 seconds, some bursts were shorter due to device error (burst length

mean 43.9sec, median 59.9sec). We were only interested in bursts recorded during flight, so following [25], we first classified bursts as either in-flight (n=193) or sitting on sea surface (n=282) by fitting a two-component GMM to the bimodal distribution of mean speeds (BIC=-625.7, log-lik=-297.44; Figure S5). Flight bursts showed high mean speed (10.89 ± 3.31 ms^{-1}) while sitting bursts showed low mean speed and variance (1.33 ± 0.61 ms^{-1}). Sitting bursts were excluded from subsequent analysis.

For all flight bursts (n=193) we identified clusters in the distribution of mean speed, power variance and E_K variance by iteratively fitting trivariate GMMs with an increasing number of clusters. Although Bayesian Information Criterion (BIC) was maximised with a 3-component model, by far the greatest BIC increase was observed between 1 and 2 component models, identifying a clear knee-point [40]. We therefore selected a mixture of 2 ellipsoidal Gaussian components as most parsimonious (BIC=-1270.09, log-lik=-585.05, df=19). The first component's high speed and low energetic variance was consistent with powered flapping flight, while the second component showed high speed and high energetic variance, consistent with wind-powered soaring (Figure 3a). Each flight burst was classified to either flap-like (n=115) or soar-like (n=78) by maximum probability. Bursts classified with under 95% probability (*low-certainty bursts*, n=74) were of intermediate energetic variance and visual inspection suggested that most contained mixtures of flight modes, although the GMM classified the majority as flap-like (n=55). However, the resolution of the available environmental covariates meant that it would not be possible to resolve finer-scale relationships between the environment and within-burst variations in flight mode. We therefore decided to classify bursts in their entirety to either flap-like or soar-like for subsequent analyses.

Summary energetic parameter values for flap-like and soar-like bursts classified with over 95% probability (*high-certainty bursts*) are reported in Table 2. High-certainty flap-like and soar-like bursts contained markedly different distributions of fine-scale in-flight power and ground speed (Figure 3b-c). Energetic dynamics within soar-like bursts generally consisted of large oscillations in power, often due to rapid E_K gains. There were large differences in the amount of time that different individuals spent engaging in different behaviours (Table 1). There were overlaps in foraging areas between birds, but no obvious visible spatial trends in the at-sea distribution of flap-like and soar-like flight (Figure S3).

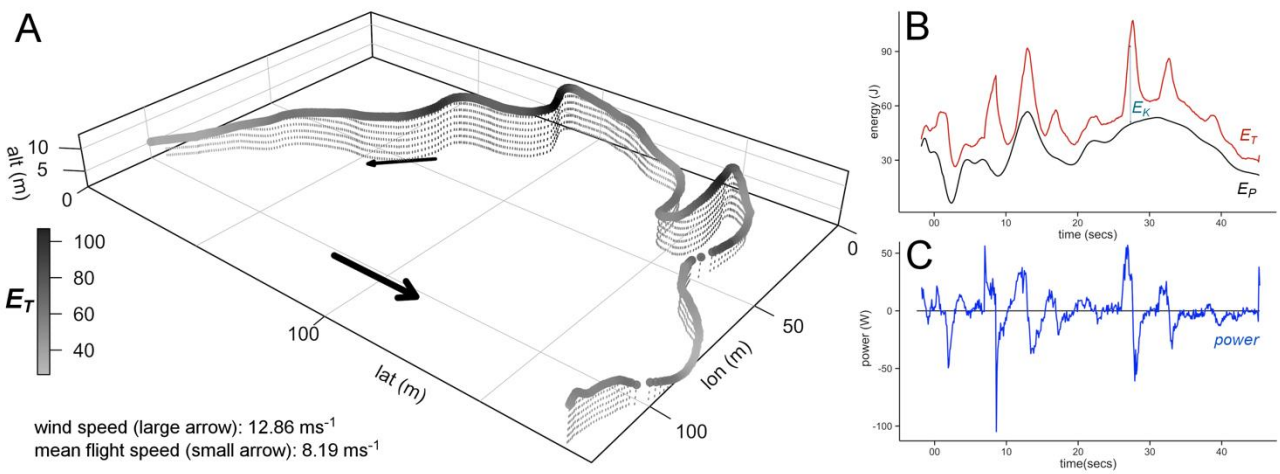

Figure 2: A high-frequency GPS flight burst. The bird's 3D path through space (A) is shown with track shaded by total mechanical energy (E_T), with arrows showing wind direction (large) and flight direction (small). Separate graphs show mechanical energy components E_T, E_P and E_K (B) and power (C) against time. This burst contains both low-power flapping and spikes in power suggesting wind energy input.

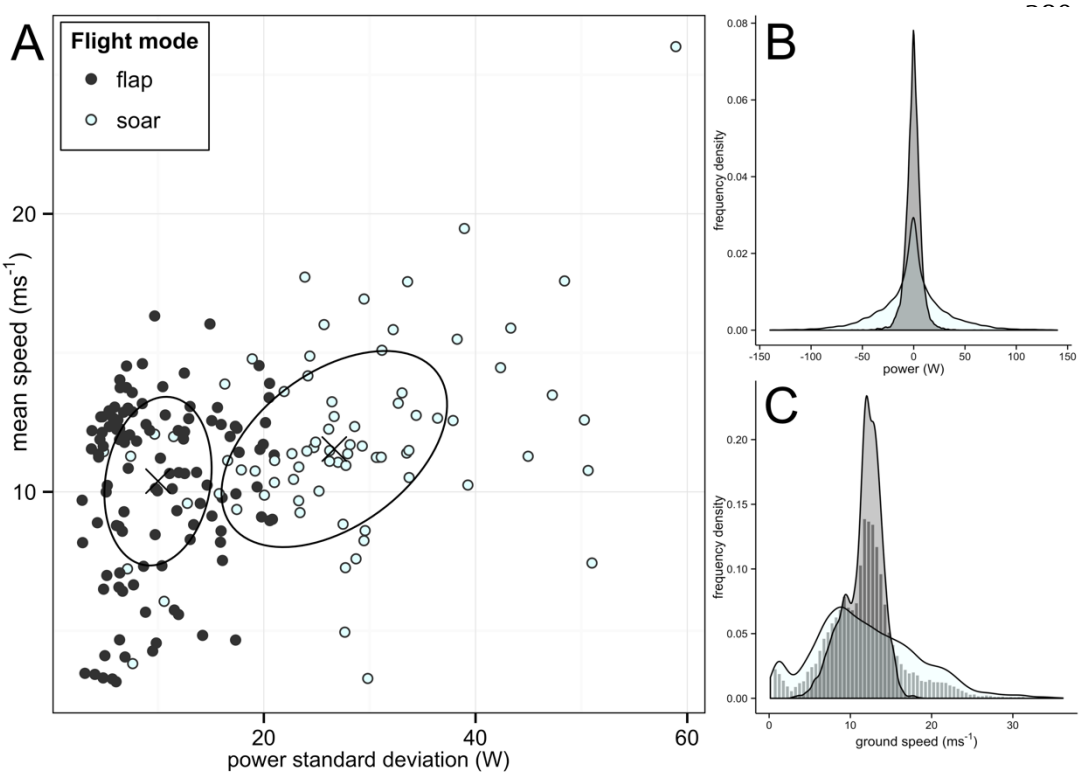

Figure 3: Energetic characteristics of flap-like and soar-like flight. ~~The~~ (A) ~~relationship~~ Relationship between burst summary parameters power variance and mean speed, ~~is shown in (A)~~ with ellipses showing modelled Gaussian components (mean+sd). (B) Density curves show within-burst distributions of fine-scale power (B) and ground speed (C) for flap-like (grey) and soar-like flight (white), produced by combining 10Hz points from all bursts classified to either mode with over 95% probability. The distribution of ground speeds across all flight bursts (both flap-like and soar-like) was trimodal (histogram in C).

Flight mode	number of bursts	mean ground speed (ms^{-1})	power variance (W) (*)	E_K variance (J) (*)	beeline distance (m)	straightness index (**)
Flap-like	60	11.46 ± 2.23	7.22 ± 2.63	4.98 ± 2.74	422.3 ± 268.3	0.88 ± 0.12
Soar-like	59	11.97 ± 3.84	30.62 ± 10.5	27.29 ± 10.68	418.0 ± 299.5	0.72 ± 0.25

Table 2: Summary ~~mechanical energy~~movement and energetic characteristics of bursts classified to flap-like and soar-like with over 95% probability (n=119). Values reported are mean ± sd. Asterisks denote a significant difference between flap-like and soar-like bursts ($p < 0.0001$), tested using either two-sided t-test (*) or Wilcoxon sum-ranks (**).

3.2. Environmental predictors of soaring

Wind speed data were accessed for 189 bursts (data for 4 bursts were missing from the METOP/ASCAT dataset, possibly because of cloud cover). Tracked birds encountered wind speeds between 1.41 and 13.69 ms^{-1}, with each bird experiencing a range of wind speeds during tracking (Table 1; Figure S10). Wind speed had a clear strong effect on power variance, with soar-like bursts with high power variance almost exclusively observed in winds above 8 ms^{-1} (Figure 4a). Mean ground speeds were mostly concentrated between 11 and 15 ms^{-1} in low winds, becoming more variable at higher wind speeds (Figure S9). Birds were more often recorded flying in crosswind (n=99) than headwind (n=57) or tailwind (n=33) (Figure 4b).

We modelled the relationship between wind speed, flight direction and flight mode using logistic mixed-effects regression, including an interaction between wind speed and flight direction and including individual and day as random effects (n=189, AIC=204.1, model outputs are reported in supplementary materials). Model deviance was significantly reduced with wind speed and flight direction included as predictors, compared to an intercept-only null model (ΔAIC=19.5; χ^2=29.5, null–residual deviance 217.57–188.11, df=5, p<0.0001). The model showed a highly significant effect of wind speed on flight mode, with likelihood of soaring increasing at higher wind speeds (~~Figure 4b~~Figure 4c). There was also a significant interaction between wind speed and flight direction, with soaring occurring less frequently in strong headwinds than in tailwinds or crosswinds (for separate plots for each flight direction, see supplementary material). The strength and significance of both these relationships increased and model fit improved when low-certainty bursts were excluded (n=119, AIC=93.9, residual deviance=77.9). The second model additionally showed a significant effect of flight direction on flight mode, with reduced soaring

in headwind compared to crosswind and tailwind. We found no significant relationships between flight mode and oceanic productivity (supplementary material S2).

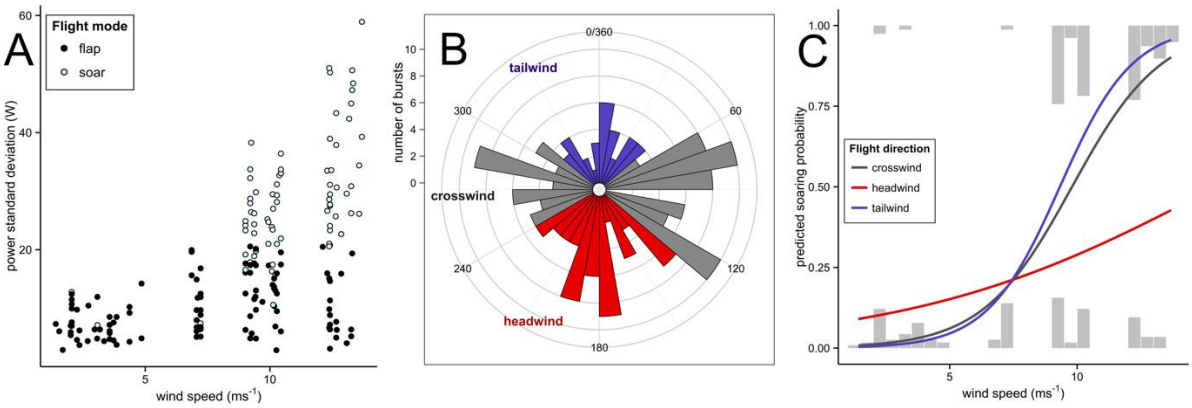

Figure 4: The relationship between flight and wind conditions, for all flight bursts for which wind data were available (n=189). (A) Relationship between wind speed and burst power variance, with flap-like bursts shown in black and soar-like bursts in white. (B) Histogram of the per-burst difference in degrees between the bird's flight direction (beeline bearing) and wind direction, where a value of 0° denotes no difference (i.e. flight direction is the same as wind direction). For modelling, flight direction was categorised as headwind (shown in red), crosswind (grey) or tailwind (blue). (C) Wind speed is a highly significant predictor of soar-like flight (logistic mixed-effects regression controlling for individual and day), with soaring less likely to occur in strong headwind than tailwind or crosswind. Grey histograms show density of wind speeds for all bursts classified as either flap-like (bottom) or soar-like (top).

4. Discussion

Ocean wind patterns are important drivers of seabird ecology and evolution [13,41], and recent research integrating information from multiple biologger types has revealed that winds ~~are~~ exert a ~~key~~ major influence on timing and distribution of foraging and migration in many species [1,8,14,15]. The relationship we demonstrate between flight behaviour and local wind conditions illuminates some of the behavioural mechanisms that underpin these large-scale patterns~~Our results show a relationship between flight behaviour and local wind conditions that sheds light on the behavioural mechanisms underpinning these larger-scale ecological trends~~. Crosswinds and

tailwinds above a wind speed threshold of around 8ms^{-1} are highly significant predictors of soar-like behaviour in foraging Manx shearwaters. While we emphasise that these results come from a population sample of 7 individuals, they support the inference that suitable wind conditions enable birds to engage in soar-like flight, which is likely to reduce overall energy costs during journeys. ~~While s~~Statistical behaviour state classification is increasingly used to analyse animal tracking data [26,33,42]. However,~~,~~ to our knowledge this is the first time such an approach has been used to both identify distinct modes of flight behaviour and demonstrate their predictive relationship to environmental conditions.

4.1. Tracking and modelling of flight behaviour

The effect of tags on study animals is a key consideration in tracking research. Previous tests with devices of equal weight reported minimal impacts on movement and reproductive success in Manx shearwaters [42], however we tracked movement at much finer temporal resolution than any previous study, and it is impossible to rule out the effects that a device weighing up to 4% of body mass could have on behaviour (e.g. [43]). Nonetheless, we observed the same responses to wind speed across several individuals that encountered both low and high winds during tracking. We suggest that although tag weight may impact flight to some degree, this is unlikely to significantly alter overall behavioural trends.

Using mean ground speed, kinetic energy (E_K) and power as variables in the GMM offered several advantages for distinguishing wind-powered from flap-powered flight behaviour. Although the relative 3D positional accuracy of successive GPS fixes is very high, absolute GPS accuracy is more reliable horizontally (used to calculate ground speed and E_K; absolute error of ± 2.5m) than vertically (used to calculate potential energy E_P). Visually inspecting all flight bursts

showed no abrupt changes in altitude that were obviously artefacts, however we opted to exclude absolute E_P values (which are derived from absolute altitude) from the GMM in order to minimise any potential effects of GPS error. Mechanical power measures the rate of energy change across each between-fix time interval t ($P = (\Delta E_K + \Delta E_P) / t$), so by including power (derived from change in altitude) as an input variable we ensured that the GMM still incorporated relative changes in E_P, an important aspect of soaring flight. For additional model validation we also independently hand-classified bursts as soar-like or flap-like based on visual inspection of their shape, and the results closely resembled model outputs (Figure S7), improving our confidence that the clusters identified by the GMM correspond to these behaviours.

The GMM clearly distinguished ~~majority~~ bursts that contained mostly flap-like ~~and~~ or soar-like ~~bursts~~movement, due to their markedly different mechanical characteristics. However, it appeared slightly biased towards classifying low-certainty bursts (those classified with under 95% probability) as flap-like (n=55) rather than soar-like (n=17), despite visual inspection suggesting that most were mixed-mode. These intermediate energy bursts mostly occurred in wind speeds above the soaring threshold (Figure S8) suggesting that our models may slightly underestimate use of soaring in wind speeds above 8 ms^{-1}. This emphasises that although a behavioural state framework is a useful abstraction for modelling relationships between flight mode and environment, Manx shearwater flight is complex and responsive to local heterogeneity in wind and wave conditions. 60-second tracked flight bursts exist on a continuum of mixed behaviours, ranging from mostly flap-like to mostly soar-like (e.g. Figure 2). This variability reflects the smaller wingspan and flap-gliding flight of this species compared to that of large soaring specialists such as albatrosses, which travel long distances without flapping their wings. Soar-like bursts occasionally showed regular E_P and E_K oscillations resembling those observed in albatrosses, albeit with shorter soar cycle lengths (5sec compared to 15sec) [22], however such

stereotyped movement was relatively uncommon (see supplementary material S4). The resolution of the available environmental covariates meant that it was not feasible to model the effect of environment on within-burst variability in flight behaviour. However, in future, either accessing wind data at a higher spatiotemporal resolution (e.g. collected using on-animal tags) or recording much longer high-frequency GPS bursts (e.g. 5-10 minutes or above) could potentially facilitate analysis of the effect of wind on flight behaviour at an even finer scale.

4.2. Flap-like and soar-like flight characteristics

Birds engaging in powered flapping flight are predicted to minimise net energy expenditure by travelling close to maximum range velocity (V_{mr}), the speed at which maximum distance is covered per unit of fuel [28]. Previous studies tracked Manx shearwaters at mean ground speeds of 10–11 ms^{-1}, slower than their estimated V_{mr} of 14 ms^{-1}, suggesting some use of wind while travelling [25,27]. Our results confirm this, and show that soar-like flight enables shearwaters to travel at equivalent mean ground speeds as flapping (Table 2). Within flap-like bursts the highest density of ground speeds occurred between 12 and 14 ms^{-1} ~~Within flap-like bursts we observed a clear ground speed peak between 12 and 14 ms^{-1}~~ (Figure 3c), with birds apparently maximising efficiency by travelling close to V_{mr}. The relationship between ground speed and airspeed varies with flight direction relative to wind; we hypothesise that birds maintain airspeeds close to V_{mr} throughout flapping, and that much of the observed within-burst variability in ground speed is due to birds flying with or against the wind, as indeed is the broader distribution of mean ground speeds observed in high winds (Figure S9).

In contrast, during soar-like flight regular kinetic energy boosts from the wind generate power levels far exceeding those available through flapping alone (Figure 3b), with maximum available

power appearing to increase as a function of wind speed (Figure 4a). Accelerating and slowing repeatedly as they change flight path and body orientation relative to wind, soaring birds cover a far broader range of ground speeds (Figure 3c) along significantly more tortuous flight paths (Table 2). Soar-like flight in Manx shearwaters involves more flapping activity than in albatrosses [13], whose metabolic costs while soaring are extremely low [18]. Nonetheless, we find that soaring shearwaters cover equivalent distances as in flap-like flight (Table 2) while spending much more time flying at closer to their estimated minimum power velocity (V_{mp}) of 7.5 ms^{-1} (Figure 3c), which strongly suggests that energy expenditure is lower during soar-like flight. The second smaller peak between 0 and 2.5 ms^{-1} emphasises the distinction between ground speed and airspeed; it corresponds to phases during soaring when birds ascend into oncoming wind, sharply decreasing in ground speed but simultaneously increasing in airspeed [22]. Birds were also more likely to soar in suitably strong tailwinds and crosswinds than headwinds, although the relative coarseness of our wind data (24-hour averaged vectors) means that these categorised directions may be inexact. This nonetheless makes intuitive sense, since soaring against strong headwind is both time-inefficient and metabolically costly [18,20].

More broadly, these insights emphasise the emerging potential of high-frequency GPS biologgers, either solo or paired with other sensor types [20,44], as tools for studying fine-scale movement behaviour in wild animals. Tri-axial accelerometers are typically used to quantify metabolic energy expenditure in tracked animals (e.g. [45,46]). However, since these measure body acceleration rather than an individual's position in space they can present challenges for studying soaring and gliding in birds, in which body posture often remains relatively fixed and much muscle work is isometric [44]. In future, combining high-resolution GPS with co-deployed accelerometer tags would enable more precise estimation of the relative metabolic costs of

different flight modes in this and other bird species, providing even more detailed insights into dynamic relationships between flight behaviour and the local environment.

4.3. Ecological relevance and future directions

Global wind patterns affect migration strategies in many ~~migratory~~ birds [6,7,14] and ~~as well as affecting~~ the foraging ecology ~~in~~ of pelagic seabirds [1,8]. Breeding and migration success may depend on minimising energy costs during these trips [1,28]. Our results support the inference that soaring in tailwinds and crosswinds above an 8ms^{-1} threshold enables Manx shearwaters to reduce flight energy expenditure, and therefore suggest a local-scale behavioural mechanism by which the wind conditions experienced by birds during flight modulate the net cost of at-sea journeys. Wind conditions are therefore likely to affect route choice, for example sufficiently high speed crosswinds and tailwinds may provide low-cost soaring corridors to foraging areas. This may contribute to the costs of foraging during reproduction, and may be an important factor to consider in future analysis of carry-over effects, e.g. [29]. Such a mechanism may also underpin some of the considerable variety in foraging routes observed during several years' tracking of Manx shearwaters around the UK [27], as well as the flexible route choice strategies of other seabirds in response to wind [15,16]. Our data provide some support for this, in that the tracked birds travelling furthest northwest towards Wales were those that encountered the strongest winds and soared the most (Table 1).

Migratory birds are predicted to evolve migration strategies that minimise energetic costs [28]. Following favourable conditions for soaring may be one behavioural mechanism by which long-term trends in oceanic wind patterns, including the persistence of stable atmospheric features, affect the evolution of migration routes and timing in the Manx shearwater and other seabirds

[8]. By identifying the wind conditions that favour soar-like flight, our results therefore present opportunities for a more predictive approach to understanding seabird life histories. We suggest that a future research direction, applying our model outputs, would be to combine global-scale wind data with the multiple years of geolocator and GPS migration tracks now collected for this species [26,27], in order to further ~~understand~~ assess how local behavioural responses to wind influence its global spatial distribution and migratory routes. Such an approach may also have conservation management implications for this and other seabirds. For example, although Manx shearwaters are generally considered low risk for collision with offshore wind turbines due to their relatively low-altitude flight [47], applying similar methods to assess the predictive relationship between wind conditions, flight behaviour and route choice in other, more vulnerable species may assist in predicting regions of present and future collision risk.

Our results also suggest that climate change-driven wind pattern shifts [10] have the potential to affect the costs of long-distance journeys in this species. Recent wind changes in the Southern Ocean have affected foraging routes and life history traits in wandering albatrosses [1], suggesting fitness impacts but also some behavioural plasticity in response to changing atmospheric conditions. However, as much smaller birds reliant on favourable winds for both foraging and migration [5], Manx shearwaters may be highly sensitive to such changes. If future global wind pattern shifts result in either increased energy expenditure during flight or extended travel times while at sea, this could have long-term population impacts on survival and reproductive success [8]. Similar impacts ~~could~~ may also be expected ~~for other~~in other pelagic seabird species, whose populations are already in global decline due to human impacts on the marine environment [48].

Conclusions

Data from on-board biologgers are fast improving our understanding of free-living animal movement. Using high-frequency GPS, here we have shown for the first time that wind speed, measured via satellite remote sensing, is an accurate predictor of soar-like flight in a wide-ranging pelagic seabird. Tailwinds and crosswinds above an 8 ms^{-1} wind speed threshold predict significantly increased likelihood of soaring flight. Both wind speed and direction are therefore likely to modulate flight costs during at-sea trips, suggesting a mechanism by which oceanic wind conditions could affect population-level foraging and migration strategies in this and other species. Our results highlight that high-frequency GPS should be considered within an emerging toolbox of tracking technologies that enable detailed quantitative study of the interactions between animal movement and the environment.

Ethics statement

Research took place under review by the British Trust for Ornithology Unconventional Methods Panel (permit C/5311) and the University of Oxford's Local Ethical Review Process.

Data accessibility

Data and code are archived on Figshare (https://figshare.com/s/bd14e3a32e3ad340e323). Link is private but will be made public on acceptance of manuscript.

Competing interests

The authors have no competing interests.

Authors' contributions

R.G. and R.F. conceived the paper, R.F. and A.S. collected the data, and R.G. and R.F. analysed the data. All authors contributed to writing the manuscript.

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Supplementary material

Please see electronic supplementary materials PDF document.

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