Adjustable wind selectivity in shearwaters implies knowledge of the foraging landscape

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Highlights

- New insights into how winds shape flight costs in a shear-soaring bird

- Shearwaters favor wind efficiency but often deviate to balance other priorities

- Low wind selectivity in weak winds suggests goal-oriented flight to foraging areas

- Windscapes may shape colony ranges via energetics and knowledge of foraging areas

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In brief

Many seabirds have evolved to use wind to fly efficiently, but this constrains travel direction. Harris et al. show how flight costs vary with the wind in Manx shearwaters and measure the degree to which shearwaters adhere to the most efficient flight paths, revealing how a seabird makes decisions between efficient flight and targeting foraging areas.

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Report

Adjustable wind selectivity in shearwaters implies knowledge of the foraging landscape

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SUMMARY

Understanding the movements of highly mobile animals is challenging because of the many factors they must consider in their decision-making. Many seabirds, for example, are adapted to use winds to travel long distances at low energetic cost[1–3] but also potentially benefit from targeting specific foraging hotspots.[4–6] To investigate how an animal makes foraging decisions, given the inevitable trade-off between these factors, we tracked over 600 foraging trips of breeding Manx shearwaters (*Puffinus puffinus*; *N* = 218 individuals) using GPS accelerometers. By first uncovering the relationships between wind and the flapping effort put into flight, we show that shearwaters, while generally wind selective, adjust their wind selectivity, apparently balancing flight costs against the benefits of travel toward known targets. This is supported by a number of scenarios that alter the balance between maximizing flight efficiency and goal-oriented flight. First, shearwaters exhibit lower wind selectivity during homing movement when constrained to target-driven navigation toward the colony. Second, when wind speeds are low, flight costs vary little with travel direction, which shearwaters respond to by reducing wind selectivity in their outbound commutes, again favoring target-driven movement toward presumably memorized foraging areas. Finally, birds are also less wind selective during longer continuous periods of flight, presumably also associated with target-oriented movement. Our findings reveal how an animal's foraging strategy can dynamically optimize the complex trade-off between efficient travel and accessing known foraging areas, implying the incorporation of prior knowledge of the cost-benefit landscape well beyond the range of what can be detected directly.

RESULTS AND DISCUSSION

Wind is a fundamental driver of flight costs in seabirds,[7–9] shaping their movement decisions and foraging strategies. Procellariiform seabirds typically favor cross- to tailwind flight, which facilitates efficient movement via dynamic soaring,[10–13] but how this influences their decisions on where to forage is unclear. To investigate how a wind-assisted seabird optimizes foraging trade-offs within the constraints imposed by the windscape and distribution of resources, we analyzed GPS-accelerometer tracks of foraging trips of a Procellariiform seabird, the Manx shearwater.[10–13] Using measurements of wingbeats and glide phases, extracted from body acceleration during commuting flights in 1–10 day foraging trips, we quantified variation in flapping effort in response to wind. Flight in strong crosstailwinds is most energetically efficient for shearwaters, achieved through both more glide-dominated duty cycles and reduced body power output during flapping. In strong winds,

the proportion of time spent flapping varies by up to 2.5-fold between head- and cross-tailwind flight (Figure 1A), whereas estimated power output during flapping decreases by up to 1.3-fold depending on wind speed and direction (Figure 1B). Shearwaters also fly at faster ground speeds in these preferred conditions (Figure 1C). Thus, selecting to fly in cross-tailwinds provides the compound benefit of being both energy and time efficient.

The degree to which flight decisions are wind selective

To estimate total energetic cost through flapping and understand shearwaters' movement decisions, we combined duty cycle and body power during flapping into a single proxy for total energetic cost through flapping, hereafter termed "total flapping output" (Figure 1D). Using the relationship between wind speed, wind direction, and flapping output, we were able to estimate the energetic cost of discrete periods of flight, hereafter termed "flight paths" (Figure 2A). By comparing the cost of real flight
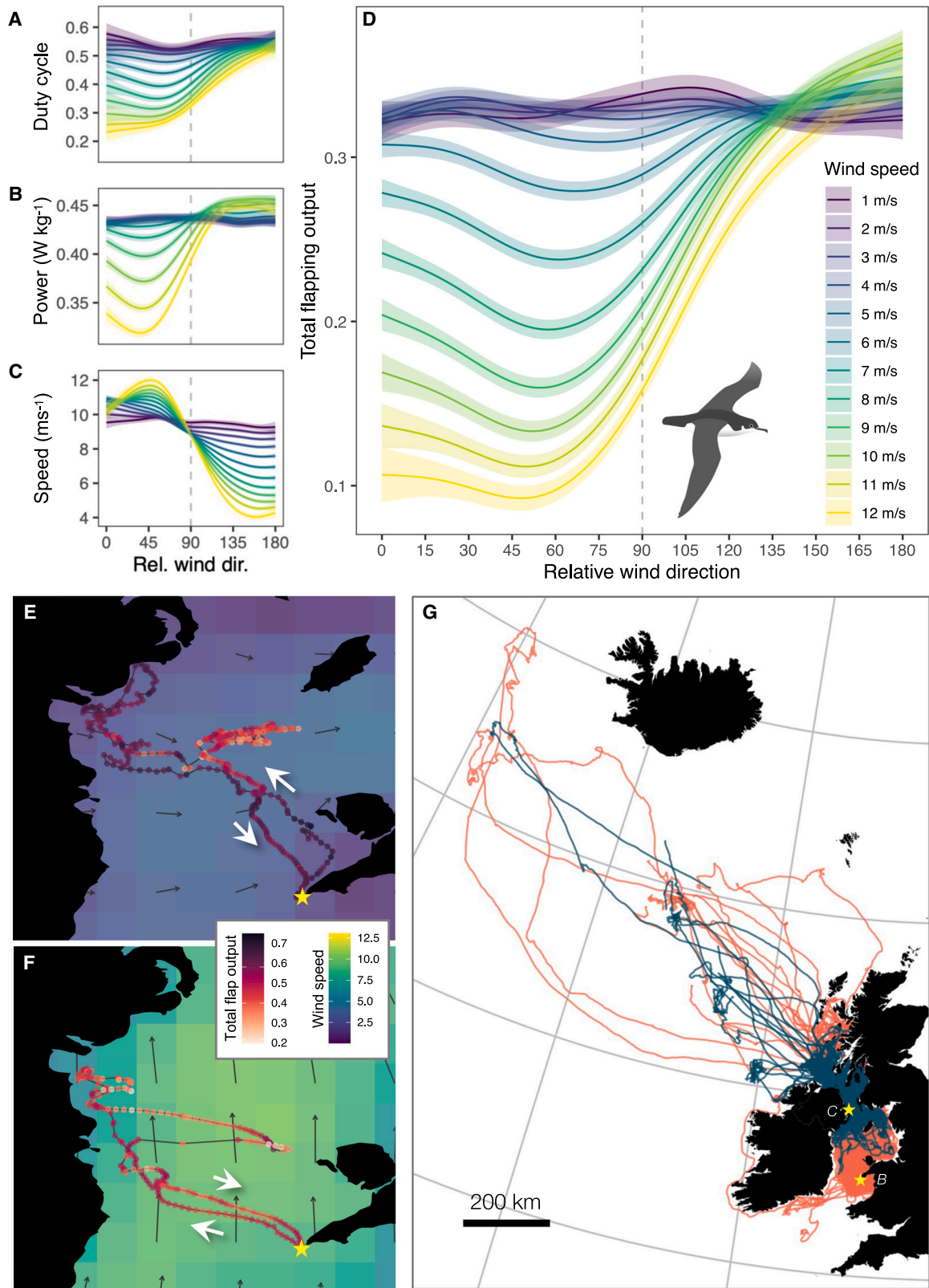
paths relative to where they fell between the highest and lowest cost of a set of 50 simulated alternative paths (Figure 2B), we estimated *wind selectivity*: this metric quantifies the degree to which a bird's flight path constitutes a decision either to fly cheaply in a constrained direction or to pay an energetic cost to fly in a direction other than the cheapest (Figure 2C).

Although Manx shearwaters do tend toward wind-selective flight overall, their wind selectivity is frequently low (<0.5 in 40% of cases; Figure 2D). While the distribution of wind selectivity is biased toward 1 (where 1 indicates a real flight path that outperformed all simulated alternatives), many flight paths perform closer to the least favorable of available options (values closer to 0). Other shear-soaring seabirds have been shown to exhibit extreme adherence to the most favorable wind-relative flight direction, consistent with a "cheap-to-fly, encounter-by-chance" foraging strategy.[3,14] However, although Manx shearwaters are known to harness energy from the wind by shear-soaring,[12] there is also indirect evidence that they target specific known foraging locations: flight behavior during the first hours of a foraging trip has been shown to predict how far from the colony a shearwater will travel, implying that birds anticipate the distance of their target area early on.[15] Other closely related shearwaters also show strong site and route fidelity, consistent with use of prior knowledge of the foraging landscape.[16] Oceanographic features like frontal zones and shelf edges provide reliable foraging opportunities for marine predators in temperate waters, resulting in the availability of prey being fairly predictable at the mesoscale.[6,17] Seabirds in the Irish Sea (including Manx shearwaters) frequently target features including the Irish and Celtic Sea fronts,[17,18] which likely aggregate their preferred prey (typically small clupeid fish[19,20]) in predictable foraging areas. Hence, Manx shearwaters appear to operate at neither extreme end of the trade-off between wind selectivity and memory-driven foraging targets, but how they optimize this trade-off has received little attention. We therefore used our wind selectivity metric to measure how wind selectivity varied within and between trips.

Trade-offs between flying cheaply and toward known targets

The trade-off between being wind selective and flying toward known targets at potentially increased cost is exemplified during homing, which is, by definition, target oriented. Intuitively, Manx shearwaters are less wind selective during inbound flights to the colony than during outbound flights (Figure 3B; Table S1). However, interestingly, we also found predictable conditions under which shearwaters exhibited low wind selectivity during outbound movements: shearwaters were most strongly wind selective when absolute wind speeds were high, during both outbound and inbound flight (Figure 3D; Table S1). The cost landscape becomes more heterogeneous in high winds (which we demonstrate in terms of the increase in standard deviation

of simulation costs with increasing wind speeds; Figure S2). Our model of flapping output under different wind conditions (Figure 1D) indicates that, above wind speeds of 4 ms^{-1}, shearwaters stand to save energy by being wind selective. However, wind selectivity gradually increases across the range of wind conditions encountered (0–12 ms^{-1}), suggesting that shearwaters frequently select flight paths less energetically efficient than the most efficient available. This implies that, when an energetic advantage for wind selectivity is available but modest, shearwaters tend to favor an alternative strategy: most likely, they instead target regions they anticipate will offer high foraging pay-offs. If shearwaters relied primarily on chance encounter to find prey, the expectation instead would be for the maintenance of wind selectivity, as this should maximize the net energetic pay-off of a foraging trip without knowledge of prey distribution. An alternative hypothesis is that birds orient randomly when wind speeds are low. Visualization of foraging trips made by the same individual departing on consecutive days and under low wind conditions (<3 ms^{-1}) reveals that, without wind influence, birds show a strong tendency to orient in the same direction as they did on their previous trip (Figure S1). All but one individual departed on their second trip along an almost identical bearing to their first (although in some cases, after initially flying in the same direction as previously, birds then went on to travel to different areas than those visited in the first trip). Together, this suggests that Manx shearwaters dynamically optimize a trade-off between flying toward known prey patches and selecting the most energetically efficient path available.

Two additional findings suggest that low wind selectivity may reflect a strategic trade-off, potentially influenced by target-driven movement. First, shearwaters are less wind selective during longer continuous periods of flight than during short flight periods (Figure 3E; Table S1). Longer continuous flight periods with few stopovers might be consistent with movements toward known targets within a trip (other seabirds have been shown to make fewer stops during homing[5]). If higher wind selectivity is associated with a more opportunistic foraging strategy, birds may stop more frequently when making wind-selective movements to sample the environment and acquire information on foraging opportunities. An alternative explanation, however, is that birds minimize take-offs and landings when these behaviors are more energetically costly, such as during weaker winds[21] when birds are less wind selective. Second, during self-provisioning foraging trips, birds become less wind selective as they get closer to home (Figure 3C). This is intuitive, given the constraint on travel direction imposed by increasing proximity to a fine-scale target, i.e., the colony. On the outbound leg, however, shearwaters appear to become more wind selective as they make increasing progress toward the furthest point from the colony. The mechanism for this is unclear, but given the relatively large spatial scale at which predictable prey patches are

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Figure 1. Shearwater flight costs during foraging trips

(A–D) Effects of wind speed and relative wind direction on (A) flapping duty cycle (proportion of each flap-glide cycle spent flapping), (B) body power (W kg^{-1}) during the flapping phase, (C) ground speed (in ms^{-1}), and (D) total flapping output, a composite measure integrating flapping duty cycle and power during flapping as a measure of total energy spent on flapping during flight. Shaded areas represent 95% confidence intervals.

(E and F) Two example foraging trips (during incubation and self-provisioning, respectively) from Bardsey in low (E) and high (F) wind conditions, illustrating the requirement for higher total flapping output in low wind conditions and greater costs incurred when flying into a headwind.

(G) All Manx shearwater foraging trips tracked from Bardsey (orange) and Copeland (dark blue) used in analyses.
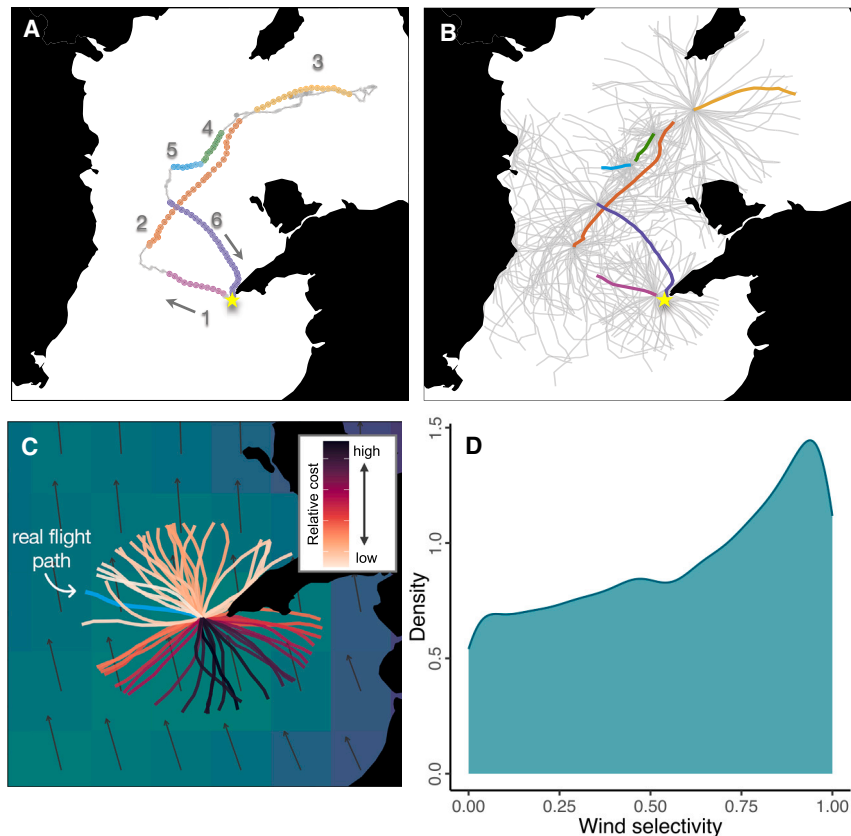
Figure 2. Analytical process for measuring wind selectivity along foraging trips of Manx shearwaters

Wind selectivity was measured for continuous bouts of flight ("flight paths") of at least 30 min identified in GPS. A single example trip is depicted for visualization in (A)–(C).

(A) An example foraging trip separated into bouts of continuous flight, numbered 1–6 from beginning to end of the trip.

(B) Random walk simulations of each flight bout to compare realized and potential flight paths.

(C) Flight path and simulations overlaying actual wind conditions (wind speed here: 6.5 ms^{-1}), with the realized flight path in the blue thicker line and simulated alternative flight paths colored by estimated relative cost (dark purple: high cost; pale pink: low cost).

(D) Density plot of wind selectivity across all shearwater flight paths. The distribution being skewed toward 1 indicates that shearwaters in general make wind-selective flight decisions, i.e., resulting in lower flapping output than alternatives. The example trip in (A)–(C) is a chick-provisioning trip from Bardsey.

expected to persist,[6] one candidate explanation might be that, as an animal approaches a large foraging area, it encounters an increasingly wider range of angular directions that still allow it to move toward (or within) the foraging area. Hence, with distance from the colony, we might expect increasing wind selectivity as the opportunity for wind-efficient flight in the direction of the known foraging region increases. This hints at the scale at which shearwaters target foraging areas being broad rather than extremely local.

If departing shearwaters can anticipate the profitability of different foraging areas at sea, the trade-off between flying in the direction of a known prey patch and the most wind-efficient direction should be revealed by birds adjusting where they fly in response to (1) the cost of flying toward profitable regions and (2) the anticipated profitability of those regions. In other words, birds should generally fly in the relatively low-cost direction but should also fly toward areas with a high pay-off. The anticipated pay-off of a specific foraging area likely relates to true prey availability (i.e., the density and depth of prey) but also an animal's certainty of its information. With continual improvements in bio-logging technologies enabling the tracking of animals over increasingly longer timescales, future work might look to examine the role of recency of foraging information (how long since an individual last sampled the foraging landscape) as a predictor of wind selectivity. Regardless of how shearwaters appraise the potential profitability of a foraging area, the anticipated pay-off of a given region would need to be higher on windier days (when the cost landscape is less uniform; Figure S2) in order to justify rejecting the most wind-selective decision.

The trade-off between wind selectivity and targeting known foraging areas may explain variation in foraging behavior between breeding stages[2] in association with different constraints on behavior. During incubation, shearwaters typically make long foraging trips (3–10 days) to recover condition following a stint of incubating the egg. During chick-rearing, by contrast, birds make short chick-provisioning trips (1–2 days), constrained by the need to frequently return to the nest to feed the chick, interspersed with long self-provisioning trips (3–10 days) while the breeding partner takes over making short trips to provide the chick with regular meals.[22] Wind selectivity patterns appear to be broadly similar among these three trip types, yet there are hints that the biological underpinnings of trip types influence how shearwaters optimize this foraging trade-off. We find no effect of wind speed on wind selectivity during the outbound leg of self-provisioning trips (Figure 3A), suggesting a shift toward the more flight-efficient end of the trade-off. Although higher winds could reduce commuting costs, interestingly, only during self-provisioning trips are high wind speeds associated with longer trip durations (Figure S3). This is perhaps unsurprising, however, because self-provisioning trips are probably when foraging trips are least time-constrained as both the chick's fat reserves and the partner's provisioning efforts buffer the effects of long trips during chick rearing (in contrast to long incubation trips, where a bird must return to relieve its fasting incubating partner[23]). Thus, at this time, making use of higher winds to travel at low cost away from the vicinity of the colony (where prey may be depleted[24]) and being broadly more wind selective may maximize trip pay-offs. Additionally, although shearwaters are more wind selective during shorter bouts of continuous flight during trips, longer trips are associated with more wind-selective flight decisions overall during chick-provisioning and self-provisioning
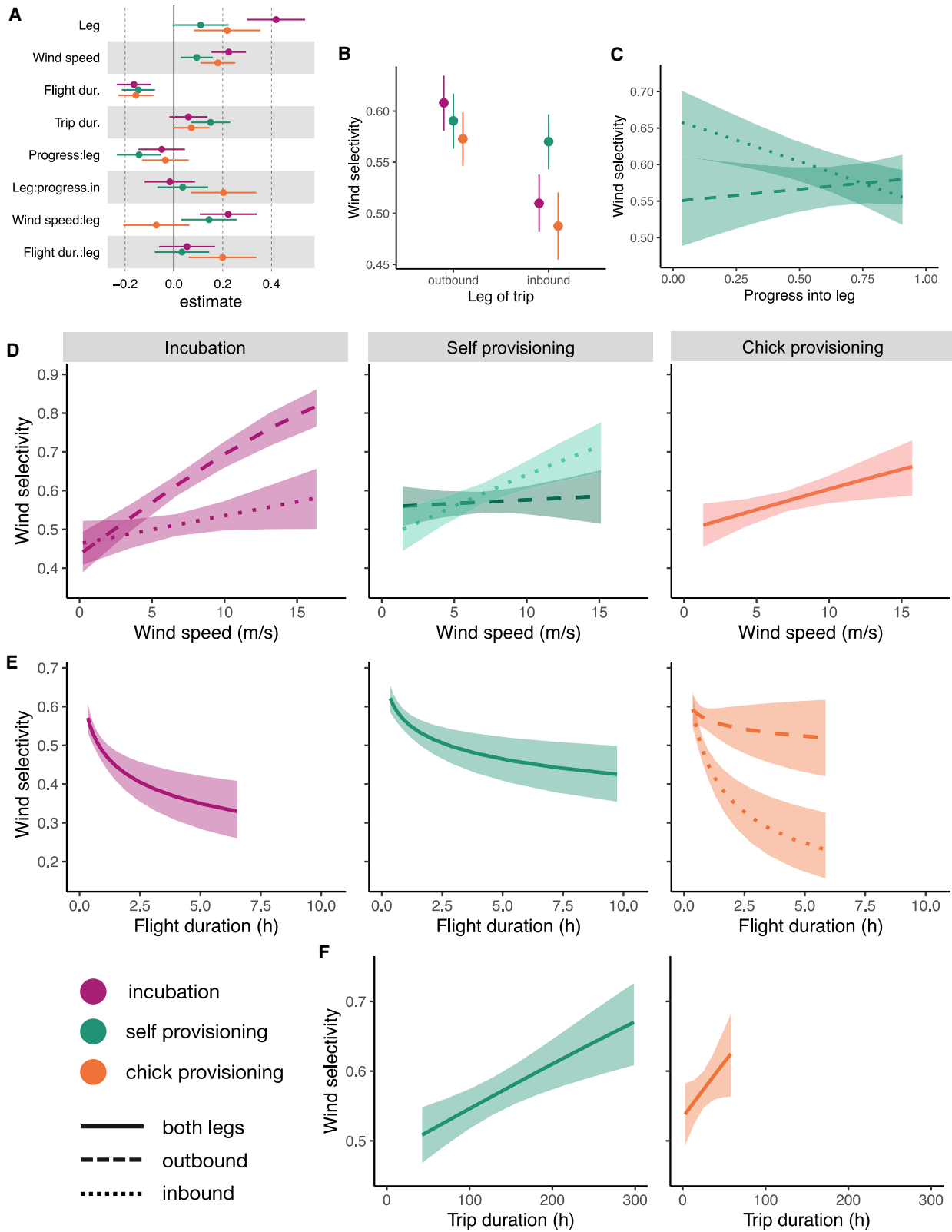
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(Figure 3F). When embarking upon longer trips with greater over-all commuting distances, birds are potentially strategically more wind selective to minimize flight costs.

The role of the windscape in colony-level foraging distributions

Despite substantial flexibility in wind selectivity, the wind-driven cost landscape clearly shapes the colony-specific foraging ranges of Manx shearwaters (Figure 1G). Notably, shearwaters from Bardsey almost never forage substantially south of the colony, entering the Celtic Sea (which begins just 100 km from Bardsey) in only two of 405 recorded trips (the southernmost-reaching of which departed under unusually strong northerly winds). This avoidance of the Celtic Sea is surprising, given that the region comprises a major foraging area for the over half of the world's breeding population of Manx shearwaters (which breed on the islands of Skomer and Skokholm[18,24]). The phenomenon of colony-level segregation of foraging areas is widespread in seabirds and cannot be attributed solely to wind, as demonstrated by spatial partitioning even between neighboring seabird colonies that encounter identical wind fields.[25–27] Nevertheless, as discussed below, colony-specific foraging ranges may be influenced by prevailing winds around the colony and the resultant effects on flight costs. Our results suggest that the influence of wind on seabird foraging ranges via flight costs may be compounded by individuals' knowledge of the foraging landscape being greater in areas that are usually efficient to reach.

Using our simulated flight trajectories, we generated maps to show areas of high- and low-cost reachability upon birds' initial departure from the colony, given the wind (Figure 4). We estimated relative cost for each cell of a $0.25° \times 0.25°$ grid by averaging the rank performance of all (real and simulated) flight paths terminating in that cell compared with their simulated counterparts. The resulting heatmaps illustrate that the prevailing winds around Bardsey Island (Figure 4) result in the waters southwest of Bardsey almost never being the optimal place to travel directly to, based on winds alone. By contrast, winds around the Copeland Islands are less concentrated in their average direction, resulting in a broader range, over time, of low-cost travel directions for shearwaters departing Copeland (Figure 4). This is consistent with the foraging distribution of Manx shearwaters from Copeland, with birds frequently making trips departing both northwest into the Atlantic and east into the Northern Irish Sea. If a wind-assisted seabird also relies on its accumulated experience of the foraging landscape to make foraging decisions, the prevailing wind direction around a given colony will shape the region(s) with which individuals from that colony become most familiar. This is evident in the persistence of shearwaters from Bardsey in traveling north even on low wind-speed days, when the flight cost of traveling south to the productive waters of the Celtic

Sea is negligibly different to that of flying north. Thus, even in seabirds that are not highly wind selective, surprisingly large effects of wind on colony-level foraging distributions may emerge.

Conclusions

To make optimal decisions about whether to be wind selective, birds require information about the predictability of both wind and foraging patches, both of which are expected to shift with climate change. Here, we demonstrate that Manx shearwaters probably forage in a windscape that is neither highly predictable (like the Southern Ocean) or highly unpredictable (like the tropics), both of which favor high wind selectivity. Forecasts predict a reduction in UK summer winds in coming decades.[28] With the majority of the global Manx shearwater population breeding along the coasts of Britain and Ireland, the effects of reduced winds on flight costs and foraging decisions might have wide-reaching consequences. Other Procellariiform species have been positively impacted by increases in wind intensity in the southern hemisphere, resulting in improvements in body condition and breeding success.[29] Evidently, average flight costs for Manx shearwaters should be expected to increase if UK summer winds reduce: birds will be required to put more flapping effort into flight and will also fly at lower ground speeds, resulting in higher energy requirements per unit distance. Foraging trips may lengthen in duration and/or reduce in distance in response. It remains unclear whether shearwaters will be able to compensate for increased flight costs by increasing their energy intake, potentially by using a less-restrictive windscape to improve their knowledge of foraging areas currently costly to access. Manx shearwaters therefore represent an intermediately wind-selective Procellariiform seabird, which will be key to understanding the consequences of changes in the predictability of the cost and resource landscapes under climate change.

Figure 3. Model terms explaining wind selectivity

(A) Forest plot showing effect sizes of predictors in wind selectivity models (terms where 95% confidence intervals do not overlap zero are statistically significant).
(B–F) Covariates found to significantly predict wind selectivity (y axes), plotted by each trip type (pink: incubation trips; green: self-provisioning trips; orange: chick-provisioning trips). Shaded areas represent 95% confidence intervals. Where significant interactions with leg of the trip (outbound vs. inbound) were detected, slopes are presented for each level (dashed line: outbound flights; dotted line: inbound flights), whereas single solid lines represent effects where no significant interaction with trip leg was detected. Only significant relationships have been plotted (hence no panel for the effect of trip duration during incubation, for example).
See also Tables S1 and S2.

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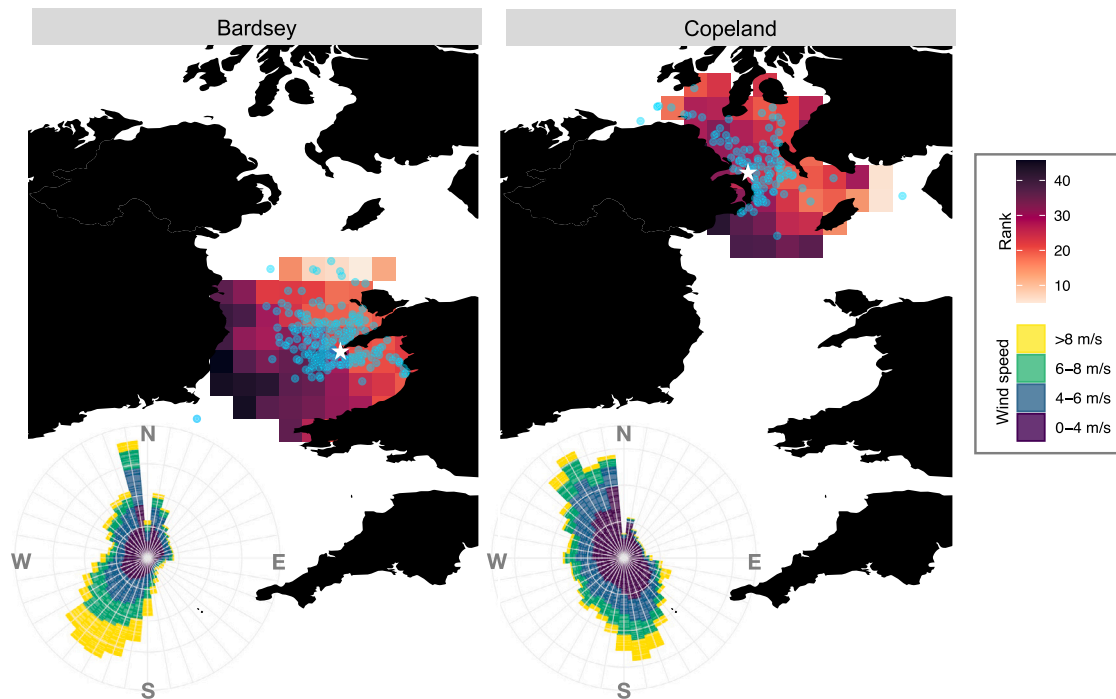## Report

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Figure 4. Average cost landscapes for all initial departures from the colony

Maps of the average cost of reaching each pixel from Bardsey (left) and Copeland (right); colony locations marked with white stars), measured in terms of the rank performance of flight path simulations relative to alternatives, averaged across three years. The color of each cell represents the average cost of reaching that cell from the colony, relative to reaching other cells the same flight distance away (dark purple: high cost; pale pink: low cost). Only simulations of the first flight bouts of foraging trips were used, and only if they began within 20 km of the colony, in order to estimate the influence of average winds on initial movements from the colony. The terminal locations of these real first flight bouts are plotted in blue points, to visualize the observed vs. expected movements given the windscape. Flight bouts from all breeding stages are included. Wind roses show average winds within 50 km of Bardsey and Copeland, respectively. Mean winds on Bardsey are much more concentrated in direction and predominantly from the southwest, whereas on Copeland the prevailing wind direction is more variable.

AUTHOR CONTRIBUTIONS

S.M.H., C.M.B., and L.S.C. conceived the study with input from all authors. Data were collected by S.M.H., S.B., T.G., P.J.L., O.P., and W.T.S. S.M.H., W.T.S., and S.B.W. processed the data, and the data were analyzed by S.M.H. S.M.H. led the writing, with support from L.S.C., and the final manuscript was produced with formative contributions made by all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
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  - Processing tracking data
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Modelling flight costs in response to wind
  - Measuring wind selectivity at decision points
  - Predictors of wind selectivity

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.12.017.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Shearwater tracking data	This study	N/A
Experimental models: Organisms/strains		
Manx shearwater (*Puffinus puffinus*)	Bardsey Island, North Wales	N/A
Manx shearwater (*Puffinus puffinus*)	Copeland Islands, Northern Ireland	N/A
Software and algorithms		
R code	This paper	https://doi.org/10.5281/zenodo.14275310

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Tracking Manx shearwater foraging trips

Breeding Manx shearwaters were tracked on Bardsey Island, North Wales (52°45'36"N, 4°47'24"W) and Lighthouse Island of the Copeland Islands, Northern Ireland (54°41'42"N, 5°31'26"W) during the breeding seasons of 2021-2023. Devices were deployed on 218 individuals over 286 deployments, with a recovery rate of 95.5% (13 tags being lost at sea before the bird was recaptured). Devices were carried for an average of 9 days (range: 1-20 days). Birds were tracked during incubation only in 2021 (N = 26 birds), and during incubation and chick rearing in 2022 (N = 108) and 2023 (N = 152). We used Axy-Trek loggers (TechnoSmart, Rome) weighing 7g, 11g or 12g (which ranged between 1.4-3.4% of bird body mass at deployment). We tested for potential effects of device size on wind selectivity and found no evidence for an effect (see Table S2). Loggers were programmed to record GPS fixes at either 5- or 10-minute intervals, tri-axial acceleration at 50Hz (or 100Hz later subsampled to 50Hz), and depth every 1-sec. Loggers were attached to birds' back feathers using TESA tape.

METHOD DETAILS

Processing tracking data

GPS tracks were processed to extract foraging trips. We first removed obviously erroneous GPS locations by applying a 30ms^{-1} speed filter[30] and then linearly interpolated tracks to 5-minute intervals using the *adehabitatLT* package[31] to standardise data resolution and account for missing fixes. Tracks with gaps in GPS data exceeding 30-minutes were split into separate sections to avoid interpolation over long unobserved periods (accelerometer and dive data during these gaps were therefore excluded from analyses). Foraging trips were defined as periods greater than 6-hours spent at least 2km away from the colony. Dives were defined using a threshold of 1m. Foraging trips were categorised as either incubation or chick rearing trips according to nest content (egg/chick) at deployment. Since Manx shearwaters are known to exhibit a dual foraging strategy after hatching,[22] chick rearing trips were further split into chick provisioning (1-2 days long) or self-provisioning (3+ days long) trips[22] (based on visual inspection of trip lengths). We examined whether shearwaters adjust their trip length depending on wind conditions at departure, separated by these trip types, in Figure S3. As a visual examination of birds' foraging decisions when departing under low wind conditions, we plotted instances when the same individual departed twice on two consecutive days when wind speeds were below 3ms^{-1} (N=8; Figure S1).

Segmenting trips into outbound and return stages

While other studies have partitioned central place foraging trips into outbound, middle and return stages based on distance and time thresholds,[32,33] most Manx shearwater foraging trips are not easily divisible in this way. Manx shearwaters do not make typical commuting trips with clear out-and-back commutes to foraging areas at the distal portion of trips, and nor do they make the classic looping trips characteristic of other procellariforms.[6] Instead, Manx shearwater trips often comprise multiple clear "commute" phases which may move in the direction of the colony and away again during the next commute, and often multiple significant foraging areas. We therefore did not aim to partition trips into outbound, middle and return segments, but instead divided trips into outbound and inbound legs before and after, respectively, the maximum distance to the colony.

Identifying at-sea behaviour

We fitted hidden Markov models (HMMs) using the *momentuHMM* package[34] to identify at-sea behavioural states at 5-minute intervals. As input variables we included step lengths and turning angles from GPS data, Vectorial Dynamic Body Acceleration (VeDBA) derived from accelerometer data, and a binary dive variable from time-depth data. VeDBA was calculated by taking the vector sum of dynamic body acceleration (after removing static acceleration resulting from the angle of the body relative to gravity[35]) and was included as a general measure of activity. Including dive data enabled us to separate two distinct foraging behaviours: active diving

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and area-restricted search (ARS) without diving. HMMs were therefore used to classify four putative behavioural states: transit flight (high speeds, shallow turning angles, high VeDBA, low probability of dives recorded); diving (moderate speeds, wide turning angles, high VeDBA, high probability of dives recorded); area-restricted search (ARS: moderate speeds, wide turning angles, high VeDBA, low probability of dives recorded); rest (low speeds, shallow turning angles, low VeDBA, low probability of dives recorded). Step lengths were represented with a gamma distribution, turning angles with a von Mises distribution, VeDBA with a logistic distribution, and diving with a Bernoulli distribution. To improve accuracy of behavioural classification we included an effect of photoperiod (daylight or darkness according to GPS time and location) on stationary state probabilities since Manx shearwaters rarely forage at night.[36] We also accounted for the inherent effect of wind conditions on birds' ground speed by including tailwind component (see details on wind data below) on mean step length distributions (following[3]). To inform initial values, we fitted 25 HMMs with initial values randomly drawn from within biologically realistic ranges, and selected the values most frequently estimated.

QUANTIFICATION AND STATISTICAL ANALYSIS

Modelling flight costs in response to wind

We calculated a proxy for energy expenditure that accounted for the fact that a flap-gliding bird can modulate its mechanical output in two ways: by varying (i) the proportion of time spent flapping, and (ii) biomechanical power output when flapping (through varying wingbeat frequency and flap amplitude[37]). Using tri-axial accelerometer data from periods of transit flight (as classified by the HMM, after disregarding the first and last 5-minutes of flight), we applied a continuous wavelet transform to raw Z-axis acceleration to extract bouts of flapping. Flap-glide cycles were identified as a bout of flapping followed by a glide phase (identified as periods of flight in between flapping bouts). Histograms of flapping duty cycle and power in the body, along with a series of other variables pertaining to variation in flight effort (flap bout length, glide bout length, flapping amplitude, wingbeat frequency) were inspected and thresholds were applied to remove unrealistic values. Flapping bouts lasted 1.18 ± 0.27 seconds and glide bouts lasted 2.06 ± 1.36 seconds on average, with whole flap-glide cycles lasting an average of 3.24 ± 1.24 seconds (values are mean±SD).

For each flap-glide cycle, we calculated flapping duty cycle as the proportion of the cycle spent flapping. Assuming that a bird's body follows a simple harmonic motion as it oscillates around its mean position during steady flight, a number of comparative variables can be calculated.[37] Mean power in the body (P_b, W kg^{-1}) during the flapping phase (termed "power in the body" hereafter) was calculated following[38] as:

$$P_b = \frac{Z_{rms}^2}{2\pi^2 f_w} \qquad \text{(Equation 1)}$$

where Z_{rms}^2 is root-mean-square (RMS) acceleration in the z-axis (dorsoventral) and f_w is wingbeat frequency (Hz).

Equation 1 can also be expressed in terms of half the peak-to-peak body displacement amplitude (B, m) which should correlate with wingbeat amplitude:

$$P_b = 4\pi^2 B^2 f_w{}^3 \qquad \text{(Equation 2)}$$

Using the RMS value of z-axis acceleration, we solve Equations 1 and 2 for B:

$$B = \frac{Z_{rms}}{\sqrt{8\pi^2} f_w{}^2} \qquad \text{(Equation 3)}$$

As a single proxy for **total mechanical work through flapping** (or "total flapping output") during a period of flight, we multiplied mean power in the body during the flapping phase by the length of the flapping phase (seconds) to get the total flapping power, and multiplied this by the flapping duty cycle. Total flapping output can be regarded as the absolute flapping power per flap-glide cycle.

We modelled the effects of wind on four variables relating to flight costs. Our primary variable of interest was (i) total flapping output. To further understand how wind influences this flight cost proxy, we also fitted separate models of the effects of wind on (ii) flapping duty cycle and (iii) power in the body during flapping. We averaged each of these three variables across flap-glide cycles within 5-minute bins between successive GPS locations of transit flight. We additionally extracted birds' (iv) straight-line ground speed (ms^{-1}) between 5-minute GPS locations to examine, in a fourth model, how ground speed relates to wind conditions. For each GPS location, we extracted wind speed and wind direction (using hourly wind data from the ERA5 reanalysis dataset; Copernicus Climate Change Service) and calculated relative wind direction (absolute difference between the bearing of the bird and the wind direction), ranging between 0° (tailwind) and 180° (headwind). We used generalised additive mixed models (GAMMs) to model the effects of wind conditions on flight costs, since the effect of relative wind direction on flight costs is often nonlinear.[3] In each model, the relevant flight cost variable (total flapping output, flapping duty cycle, power in the body, or ground speed) was fitted as the response variable, with fixed effects of wind speed, relative wind direction, the tensor product interaction between wind speed and relative wind direction, and a random effect of individual. GAMMs were fitted in the *mgcv* package[38] using thin-plate regression splines with shrinkage for all predictor variables, with the gamma parameter set to 1.2 to avoid overfitting.

Measuring wind selectivity at decision points

We interpret the beginning of a continuous flight bout as a decision point (*sensu*[39]) when shearwaters decide where to direct their next substantial movements with respect to their target (a foraging patch, or their breeding colony) and current wind conditions. Flight bouts were identified as continuous periods of commuting flight of at least 30 minutes (N = 4,126). To measure wind selectivity at these decision points we applied a simulation-based approach as follows: we generated alternative realistic movement paths from the decision points, equal in length and movement parameters (step lengths and turning angles) to the real flight path, initially departing in any direction from the decision point (but avoiding land). The initial direction from any given decision point was randomly selected (drawn from a uniform distribution bounded between 0 and 360), with a step length drawn from the original distribution of step lengths in the corresponding real flight path. This process was repeated in a stepwise fashion for all steps of the real path, with turning angles also drawn from the original distribution observed in the real path. Step lengths and turning angles were drawn without replacement such that simulated paths would be of equal length to real paths. As shearwaters do not routinely fly over land,[40] we constrained simulations to avoid land by testing whether each new step intersected land using a simplified shapefile for the UK and Ireland in which estuaries are slightly smoothed to prevent simulated shearwaters getting "stuck" in inlets. In cases where a step intersected land we randomly selected a new turning angle from the available distribution, aborting the simulation if all possible turning angles resulted in contacting land. Only simulated flight paths matching the length of the real flight path were retained. We generated 100 simulations of each path and randomly selected 50 complete simulations of each path for subsequent analyses (fewer than 50 complete simulations were generated for 7 flight paths, which were disregarded in subsequent analyses).

Wind conditions were extracted along real and simulated flight paths. We then estimated the relative energetic cost of flying each step by predicting total flapping output as a function of the encountered wind conditions and the required ground speed. This required fitting an additional GAMM to those listed above, including the three-way interaction between ground speed, wind speed and relative wind direction. The total cost of each simulated flight path was taken as the sum of total flapping output along the entire length of the flight path. For each flight path, we then calculated wind selectivity as where the performance of the real flight path fell relative to the range of performances of simulated flight paths: in other words, if the real flight path resulted in the lowest estimated total cost compared to all of its corresponding simulations, wind selectivity would be equal to 1, and if the real flight path had the highest estimated total cost compared to all simulations wind selectivity would be equal to 0.

To assess how the uniformity of the cost landscape changed with increasing wind speeds, for each flight path we calculated the standard deviation of the total estimated costs of each simulation and compared this to the mean encountered wind speed. We tested this relationship using a GAMM with standard deviation of cost as the response variable and wind speed as a fixed effect, with bird identity and trip identity included as random effects. The predictions from this GAMM are presented in Figure S2.

Predictors of wind selectivity

Wind selectivity was modelled using mixed effects ordered beta regressions (which fit continuous data in the closed interval [0,1]) using the *glmmTMB* package.[41] Separate models were fitted for each trip type (incubation, self-provisioning, chick provisioning). Fixed effects included leg of the journey (outbound vs. inbound), wind speed, flight bout duration (hours), and trip duration (hours). We included the interaction between leg of the journey and progress into the leg (as a percentage, on the outbound leg beginning at 0% at the colony and 100% at the end of the leg and vice versa on the inbound leg), and also included two-way interactions between leg and wind speed, leg and flight bout duration, and leg and trip duration. Bird identity and trip identity were included as random effects. One extreme observation was removed (a flight bout >18 hours long) and flight bout duration was log transformed. Flight bouts from incomplete trips (i.e. during which logger batteries expired before the bird returned to the colony; n = 1,037) were removed prior to analysis owing to missing values for some variables (leg and progress into the leg). All variables were standardised to aid model fit. All combinations of fixed effects were tested in a set of 44 models, from which model-averaged parameter estimates and their confidence intervals were estimated to assess statistical significance (where confidence intervals did not overlap zero). Akaike weight-averaged marginal and conditional R^2 values were calculated for each model set using the *performance* package.[42] Figures show estimates and confidence intervals from the best performing (lowest AIC) model containing all significant predictors.