A central place foraging seabird flies at right angles to the wind to jointly optimize locomotor and olfactory search efficiency

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Abstract

To increase the probability of detecting odour plumes, and so increase prey capture success, when winds are stable central place foraging seabirds should fly crosswind to maximize the round-trip distance covered. At present, however, there is no empirical evidence of this theoretical prediction. Here, using an extensive GPS tracking dataset, we investigate, for the first time, the foraging movements of Bulwer's petrels (*Bulweria bulwerii*) in the persistent North Atlantic trade winds. To test the hypotheses that in stable winds petrels use crosswind to maximize both the distance covered and the probability of detecting olfactory cues, we combine state-space models, generalized additive models and Gaussian plume models. Bulwer's petrels had the highest degree of selectivity for crosswinds documented to date, often leading to systematic zig-zag flights. Crosswinds maximized both the distance travelled and the probability of detecting odor plumes integrated across the round-trip (rather than at any given point along the route, which would result in energetically costly return flight). This evidence suggests that petrels plan round-trip flights at departure, integrating expected costs of homeward journeys. Our findings, likely true for other seabirds in similar settings, further highlight the critical role of wind in seabird foraging ecology.

Keywords

Bulwer's petrel; central place foraging; flight behaviour; olfaction; wind; zig-zag

1. Background

Animals should minimize the energetic costs of movement during foraging while maximizing caloric intake to maximize net energetic gain [1–3]. Foraging strategies that maximize net energy intake take many forms depending upon a species' ecological niche and physiological and morphological adaptations. One very common constraint to bouts of foraging is found in species that must return to a "central place", usually to provide care for altricial progeny left at a rookery, nest, or den. Such species make foraging trips that last from a few minutes to a few days, but must return to the site from which the foraging trip originated [4].

The foraging movements during breeding of seabirds are made from central places. This includes species from the order Procellariiformes (tube-nosed seabirds; the albatrosses, petrels, and shearwaters). Members of this order spend most of their lives on the wing in the open ocean, returning to land only a few months per year to breed [5]. During breeding seasons, despite the constraint of a central place, foraging trips of seabirds can still cover thousands of kilometers [6]. This striking motility is underpinned by an exceptionally efficient flight strategy known as "dynamic soaring", whereby seabirds exploit the wind velocity gradients ("wind-shear") close to the surface of the ocean, ascending into the wind and descending with the wind, thus gleaning aerodynamic kinetic energy [7–11]. Furthermore, while wind–shear soaring provides most (~80–90%) of the total energy for sustained soaring [8], additional energy can be extracted by seabirds by exploiting wave-induced features of the wind fields and localised updrafts produced by wind blowing over waves [8]. When carrying out the swooping manoeuvres characteristic of dynamic soaring [12], seabirds exhibit a movement orientation bias relative to wind direction ("anemotaxis"), typically using crosswinds (i.e. blowing perpendicularly to the bird heading) and quartering-tailwinds (i.e. blowing from behind, at an acute angle to the bird direction of movement) [11] to maximize their traveling speed [9,13,14] and minimize their energy expenditure [9,15].

Wind direction and intensity greatly impact advective odor dispersal, shaping the odor landscape on the surface of the ocean [16,17]. Many procellariiform seabirds use their highly developed sense of smell to locate widely distributed food patches across long distance foraging flights [16,17] as well as to identify partners and nests [18]. In fact, Procellariiformes have among the largest olfactory bulbs of birds [19]. This is particularly true for nocturnal seabirds, which have a relatively larger olfactory bulb size than diurnal species [20]. To inform olfactory foraging, seabirds use anemotactic flight strategies [16]. For instance, when searching for food, wandering albatrosses (*Diomedea exulans*) flew using crosswinds and quartering-tailwinds to maximize the probability of crossing an odor plume, and are able to detect odor sources at ranges of up to 20 km [17]. Evidence of crosswind odor plume search strategies have been documented in other taxa, such as insects [21,22].

The effect of wind on the costs of movement of central place foraging seabirds has been widely investigated from both theoretical [23] and empirical [e.g. 6,9,12] perspectives.

Based on theoretical models, crosswind flight is predicted to be the optimal anemotactic strategy in a wind field that remains constant over the spatial and temporal domain of use [23]. These theoretical predictions are fairly intuitive, because birds flying with the assistance of advantageous tail winds during the outward section of the flight would have to face the costs of returning to the colony with headwinds. Due to the longer duration of the headwind homeward flight and the extra food load, the costs would exceed the benefits, making this strategy less profitable than crosswind flight [23].

Thus, in stable and uniform winds, crosswind flight is predicted to be the most advantageous anemotactic strategy for seabirds to both minimize the energetic flight costs of combined outbound and inbound segments of foraging trips from central places, while also maximizing the number of odor plumes crossed for a given distance travelled. At present, no empirical observations have provided full support for these theoretical predictions and, in fact, for the reasons outlined below, key deviations from these predictions have instead been observed in other systems.

Historically, the geographical coverage of seabird tracking studies has been biased toward high latitude regions, which are characterized by much more variable wind conditions. In such conditions, instead of using crosswind, seabirds can carry out fast, long looping routes orienting at the most favorable angle with respect to the local wind conditions throughout the foraging trip [e.g. 9]. Use of wind fields by seabirds living in tropical and subtropical latitudes, where predictable trade winds prevail [24], is less well understood [25]. Tracking studies have also historically tended to focus on large seabirds able to carry heavy early generation tracking devices [24]. These large species are typically diurnal, feed on epipelagic prey, and show some levels of foraging site fidelity to productive areas associated with seamounts, shelf breaks, upwelling regions, and frontal zones [26–29]. In these situations, advantages of commuting to these areas may outweigh the sub-optimal energetic subsidies available during the commute from central places [9,13]. Furthermore, upon reaching productive areas, seabirds may engage in area-restricted-searches (ARS), performing slower and more tortuous movement bursts [16]. During ARS, birds may deviate from a crosswind flight strategy by pursuing visual cues regardless of the wind conditions experienced, for instance, by directing their flight towards other foraging seabirds [30], fish schools, or fishing vessels [31,32]. Considerably less is known about the foraging ecology of smaller nocturnal seabirds feeding on mesopelagic prey. These birds may rely on visual cues to a limited extent, feed opportunistically *en route* on less predictable food resources (such as vertically migrating prey present near the ocean surface mostly at night) and do not forage in large aggregations. These features suggest that they should maximally benefit from crosswind flight to facilitate olfactory food search.

Here, for the first time, we analyze the flight behavior and use of wind by Bulwer's petrel (*Bulweria bulwerii*), a ca. 100-g nocturnal [33,34] specialist predator of mesopelagic prey [35] foraging in the persistent North Atlantic trade winds. The ecological features of this study system make it particularly well-suited for investigating the role of wind in shaping

the movement patterns of petrels and other similar seabirds. Recent work using geolocation devices found that breeding Bulwer's petrels use waters both within and beyond the northern boundary of the trade winds belt [33]. This feature thus provides enough environmental contrast to test if individuals adjust their flight strategy depending on whether their central place foraging trips are performed only in predictable trade winds or if their strategy changes when trips move beyond the trade winds belt and into less predictable wind fields. Specifically, we assessed support for the following hypotheses:

H1) Birds performing central place foraging trips in persistent and predictable wind fields carry out trips orienting at 90° (orthogonally) to the prevailing trade winds. We predict that this preference for crosswind flights would allow birds to maximize the distance covered per unit time and minimize the energetic costs of round-trip locomotion. We also predict that, when birds use areas characterized by a higher variability in wind conditions, they would sustain their trips exploiting more assistance from the wind (i.e. a higher tail wind component), when available.

H2) Birds performing crosswind flights maximize olfactory search information by optimizing the probability of detecting odor plumes. We predict that birds exploiting olfactory cues throughout their flight would consistently show a preference for crosswinds both during day time (when visual cues can be used more extensively) and darkness (when visual cues are limited or absent). Flying perpendicular to prevailing winds should maximize the distance at which a source can be detected and the overall area scanned using olfaction along the route.

2. Methods

2.1 Data collection

We deployed GPS loggers on incubating Bulwer's petrels from colonies at Deserta Grande and Selvagem Grande (Madeira, Portugal) during three breeding seasons (June-July of 2015, 2016 and 2021). We used Pathtrack (https://www.pathtrack.co.uk) nanoFix-GEO GPS-loggers (weight of 2.3g), corresponding to ca. 2.3% of adult petrels body mass. Tags were programmed to record locations on two schedules. In the first, loggers recorded points every hour, which allowed for analysis of flight throughout the entire foraging trips from the moment of departure to return and distinguish between "nearby" and "distant" trips. In the second, loggers recorded locations every 3 minutes for six hours each day, which allowed us to investigate wind use at a high resolution and with minimal chance of missed state-changes. Prior to analysis, all the tracks were linearly interpolated using the package adehabitatLT [36] in R software [37] to impute missing data. The extent of interpolation was minimal (less than 2% of the points were imputed) (electronic supplementary material S1).

The wind raster files were downloaded from the ECMWF ERA-5 database (https://cds.climate.copernicus.eu/cdsapp), at a spatial resolution of 0.25° and temporal resolution of 1 hour. The following variables were calculated for each GPS relocation: wind direction (in degrees), wind intensity (ms^{-1}), tail wind component (hereafter "TWC", calculated as in [38]), and wind direction relative to the bird bearing (hereafter 'Δangle', calculated as in [13]). Δangle ranged from a minimum of 0° (tail winds, aligned with the direction of movement) to a maximum of 180° (head winds, blowing in the opposite direction of movement).

2.2 Movement analysis

We fit discrete-time hidden-Markov-models (HMMs) using the R package momentuHMM [39] to classify the behavioral states of the petrels along the tracks, separately for the 1 h and the 3-min datasets. To improve movement behaviour classification, we accounted for the intrinsic effect of TWC on the mean parameter of the step length distribution, for both the travelling and searching states (electronic supplementary material S2). To decode the sequence of behavioural states of the Markov chain most likely to have produced the observed data given the fitted HMM, we used the Viterbi algorithm [40]. We assumed that, along the 1 h resolution tracks, the petrels were in one of two behavioral states: "transit", in which the underlying drive is to move at high speed in a persistent heading; or "search", in which the drive is to search for food upon entering a foraging patch [41]. In the 3-min resolution tracks, we assumed that the petrels were in one of these three states: "in flight", when the birds spent the entire move step flying; "on water", when the animals spent the entire move step sitting on the water surface to ingest and process food or rest; and "mixed", an intermediate state in which the animals spent part of the step in flight and part on the water, indicative of foraging attempts (electronic supplementary material S2).

2.3 Wind use analysis

The distribution of Δangle for the different states in the 3-min and 1 h resolution tracks was calculated, quantifying separate Δangle distributions for points recorded during day and night. The analysis subsequently evaluated the effect of wind on ground speed of the petrels. For this part of the analysis, we used only segments of the 1 h resolution tracks that were classified by the HMM as "transit". When birds were in this state, we assumed that the relationship between the wind and ground speed was only minimally affected by other activities, such as searching for food or resting. We fit generalized additive mixed effect models (GAMMs, hereafter referred to simply as "wind model") with the mgcv package [42] in R to quantify the effect of Δangle, wind intensity and their interaction on the ground speed attained by transiting petrels along the 1-h resolution tracks. The best set of candidate variables to retain in the GAMM was selected based on AIC [43] (electronic supplementary material S3).

2.4 Odor plume model

The objective of this analysis was to evaluate how the effective area searched using olfaction is affected by the Δangle of flight relative to wind direction and wind intensity. It

is important to highlight that, in this analysis, we do not consider the spatial location of the odour source (i.e. the prey). Rather, the objectives of the analysis are the following: first, to estimate the theoretical instantaneous range at which prey can be detected using olfaction (i.e. the "olfactory bandwidth", see below) by birds flying under a range of Δangle and wind intensity values; second, to evaluate how the theoretical area scanned using olfaction by birds is affected by the predicted "olfactory bandwidth" and ground speed attained in given Δangle and wind intensity values. To do this, we built theoretical Gaussian plume models [44] (hereafter referred to as "odor plume models") to analytically describe the wind-driven advection of odor plumes. We developed the odor plume model with constant emission rate from a source on the water surface, diffusivities along the y- and z-axis of 1000 m^2s^{-1}, constant decay and advection with the flow of a constant and uniform wind. Under these parameters, the theoretical odor plume models were used to quantify the concentration of odor molecules in every cell (with resolution of 5 m^2) of a 20 km^2 grid, as a function of wind intensity and distance (on the x- and y-axis) from the odor source. We assumed that the birds could detect smell when it decayed to $2*10^{-4}$ of the concentration measured at a distance of 1 m from the source. This choice yielded oval contour lines where the smell was detectable up to a maximum distance from source of approximately 5 km, which is consistent with the detection distance documented in albatrosses [17]. A set of odor plume models and resulting oval smell detection contour lines were generated with wind intensities ranging from 1 to 15 ms^{-1}. Then, integrating the results from the odor plume model with the predictions from the wind model (i.e. the predicted ground speed attained at a given Δangle and wind intensity), we calculated two key quantities. First, we calculated the theoretical "olfactory bandwidth", i.e. the maximum distance from the source at which the birds are predicted to detect the prey smell, for each value of Δangle and wind intensity, calculated applying trigonometric formulae (fig. 1). Second, we calculated the theoretical area (km^2) scanned by olfaction by a bird flying at a given Δangle and wind intensity during one movement step (1-hour), calculated by multiplying the olfactory bandwidth by the predicted distance covered (electronic supplementary material S3). A sensitivity analysis was carried out, which showed that the results obtained on the effects of Δangle and wind intensity on the area scanned are robust to the parameter specification (electronic supplementary material S3).

2.5 Track simulation: distance covered and area scanned

We applied a simulation framework to investigate whether, along the realized trips, birds: 1) maximize their speed; and 2) maximize the area scanned using olfaction along their entire round-trip foraging route from a central place. In short, a set of "random" and "rotated" simulated tracks were designed, which were equivalent (i.e. covering the same distance) to their corresponding real tracks, but along these simulated routes the birds travelled at a different Δangle. We compared the duration and the area olfactorily scanned along the simulated trips to the duration and area scanned throughout the real trips (electronic supplementary material S4).

3. Results

3.1 Movement analysis

Bulwer's petrels exhibited a large foraging range during breeding (see [45] for a comparison on other breeding Procellariiformes foraging ranges). Two high-usage areas were identified: a "nearby" area, located off the coasts of the Canary islands and West Africa, within the trade winds belt; a "distant" area, encompassing the waters to the northern edge of the trade winds belt and beyond, to the north of Azores, reached by the birds through clockwise looping trips (fig. ESM1 in the electronic supplementary material). The tracks showed a high degree of movement directionality. The birds mostly flew at constant heading between few sharp turning points, resulting in a series of zig-zagging trajectories. This is evident both in the 1-h resolution tracks (particularly off the coasts of the Canaries and West Africa, but also near the coasts of the Azores) and in the 3-min resolution tracks (fig. 2), in which the petrels often did not change heading during the whole duration of the 6 hour segments. On average, the complete 1-h resolution foraging trips of Bulwer's petrels (n = 18 complete tracks) lasted 11.5 days (s.d. 1.8 days). The average total distance travelled was 4143.6 km (s.d. 981.5 km) and the average maximum distance from the colony was 1137.9 km (s.d. 605.1 km). The maximum distance from the colony was not significantly correlated with the temporal duration of the trips (Pearson's correlation, $r16 = -0.04$, $p = 0.89$). An average of 52% (s.d. = 18%) of the relocations were classified as searching. Overall, both the sections of the tracks classified as transit and search were characterized by a high degree of movement directionality. Specifically, the mean turning angle was equal to -0.4° (circular standard deviation = 30.8°) for the transit state and -1.4° (circular standard deviation = 76.3°) for the search state. The average speed during transit was 22.2 kmh^{-1} (s.d. = 5.5 kmh^{-1}) whereas birds in the search state flew at an average speed of 9.06 kmh^{-1} (s.d. = 6.1 kmh^{-1}). Along the 3-min resolution tracks (fig. 2) the average ground speed was equal to: 26.4 kmh^{-1} (s.d. 7.2 kmh^{-1}) when birds were in flight; 3.1 kmh^{-1} (s.d. 3.5 kmh^{-1}) when they were on the water; and 19.5 kmh^{-1} (s.d. 5.5 kmh^{-1}) when they were in the "mixed" state. The 3-min resolution tracks also showed high movement directionality. Specifically, the turning angle of the birds was equal to 0.1° (circular standard deviation = 20.8°) when in flight; -0.4° (circular standard deviation = 70.5°) when the birds were sitting on the water; and 0.5° (circular standard deviation = 28.9°) when the birds were in the "mixed" state.

3.2 Wind use analysis

The petrels exhibited an extreme degree of selectivity for crosswinds (table 1 and fig. 3). This was evident both during the "in flight" and the "mixed" sections of the 3-min resolution tracks, but also along the "transit" and "search" sections of the 1-h resolution trips, resulting in strikingly narrow Δangle density curves, particularly compared to the wind use of other procellariiform seabirds in the region (fig. 3b). When "in flight" along the 64 tracked flight bouts at 3-min resolution, petrels mostly flew orienting almost perfectly orthogonally with respect to the wind (median Δangle = 89.9°), spending 64% of their "in flight" time flying at Δangle between 70° and 110°. Similarly, when in the "mixed" state,

they used crosswinds, flying at a median Δangle of 85.9° (table 1 and fig. 3a). The wind use along the 1-h resolution tracks (comprising a total of 22 trips, of which 9 "nearby" and 13 "distant") is largely consistent with the findings described above (particularly so for the "nearby" trips). The petrels showed a preference for crosswind flight, both during the transit and the search state (table 1 and fig. 3b). The Δangle used by the birds along the "nearby" and "distant" 1-h resolution trips was significantly different (Mann-Whitney-Wilcoxon Test, $p < 0.001$). The petrels had a higher selectivity for crosswind along the nearby trips, whereas their wind use shifted towards more quartering-tailwinds during the distant trips (table 1). Moreover, the TWC experienced along the nearby and distant trips was significantly different (Mann-Whitney-Wilcoxon Test, $p < 0.001$); specifically, along the distant trips the birds travelled with a stronger support from the wind (median TWC = 1.9 kmh^{-1}; interquartile range=0.1–3.7 kmh^{-1}) compared to the nearby tracks (median TWC = 0.2 kmh^{-1}; interquartile range=-1.9–1.8 kmh^{-1}). Overall, the birds consistently used crosswinds along the 3-min resolution tracks, both during day and night (table 1), resulting in Δangle values not significantly different (Mann-Whitney-Wilcoxon Test, $p = 0.51$). This result was also true for the 1-h resolution tracks (Mann-Whitney-Wilcoxon Test, $p = 0.54$) (table 1).

The results of the wind model based on the locations classified as "transit" showed that, at each movement step, the petrels are predicted to attain highest ground speed with favorable tail to quartering-tailwinds. Specifically, the wind model retained Δangle, wind intensity and their interaction as significant predictors of ground speed. The ground speed was non-linearly affected by Δangle and wind intensity, with a maximum speed attained by the birds at values of Δangle ≈ 30°, particularly when traveling with stronger winds (fig. 4a). The results of a wind model fitted to the 3-min resolution tracks are largely consistent (electronic supplementary material S3).

3.3 Odor plume model

For all wind intensities, the olfactory bandwidth ("C2" in fig. 1) is maximum for Δangle values of 90° (fig. ESM4 in electronic supplementary material). At low wind intensities, when the predicted effect of wind on the ground speed of the petrels is minimal, a Δangle of 90° maximizes the area scanned (km^2 in 1-h) by the olfactory searching birds (fig. 4b). As the wind intensity increases, the oval smell detection contour becomes stretched along the direction of wind flow (fig. ESM3 in electronic supplementary material). Furthermore, for increasing wind intensities, the birds are predicted to attain higher speeds with favorable tail to quartering-tailwinds, whereas the use of crosswinds results in lower speeds. In turn, at intermediate (e.g. 7 ms^{-1}, which is the average wind intensity experienced by the petrels along the 1-h resolution tracks) and high (e.g. 15 ms^{-1}) wind intensities, the peak of the theoretical area scanned shifts towards Δangle values < 90° (between 60° and 65°, fig. 4b).

3.4 Track simulation: distance covered and area scanned

The real tracks realized by the transiting petrels were significantly faster than the random (paired t-test, $t = -5.03$, d.f. = 17, $p < 0.001$) and rotated trips (paired t-test, $t = -3.66$, d.f. =

17, $p = 0.002$). The real duration was, on average, 175 h and 211 h (i.e. 136% and 164%) faster than the duration of the respective random and rotated trips. The area scanned throughout the real trips was also significantly wider than the area scanned along the random (paired t-test, $t = 3.11$, d.f. = 17, $p = 0.006$) and rotated (paired t-test, $t = 7.35$, d.f. = 17, $p < 0.001$) tracks. More specifically, the area scanned along the real trips was on average 646 km^2 and 1304 km^2 (i.e. 5% and 11%) wider than the area scanned along the respective random and rotated trips (fig. ESM6 in electronic supplementary material).

4. Discussion

Bulwer's petrels have a higher degree of selectivity for crosswinds than any other seabird tracked to date. This strategy, exhibited both when in transit and searching, and consistent across different observation resolutions of our tracking dataset, is striking if compared to the wind use of other procellariiform seabird populations from the same region (fig. 3b and electronic supplementary material S2). Our results show that crosswind flight enables the birds to maximize both the distance covered and the area olfactorily scanned throughout their trips. Furthermore, for the first time, we document an emerging property (discussed below) of the central place foraging trips of the petrels, underpinned by the high selectivity for crosswinds: a systematic zig-zag flight, both during the transit and the search sections of their tracks.

4.1 Crosswind flight to maximize distance covered in stable winds

Our results provide strong empirical support for the hypothesis that crosswind flight allows petrels to maximize the distance covered throughout their central place foraging routes (H1). Bulwer's petrels are predators of mesopelagic prey [35] and do not consistently target predictably rich foraging hotspots [33]. Rather, they forage over deep oceanic waters on unpredictable prey at coarse (1–100 km^2) and meso scales (100–1000 km^2), covering as much distance as possible to maximize the probability of opportunistically finding prey along their routes.

Here we clearly show that crosswind does not maximize the ground speed along each movement step. As predicted by the wind model, birds fly the fastest with quartering-tailwinds, which aligns with the findings on the speed and energy expenses of other dynamic soaring seabirds, such as albatrosses and gadfly petrels [6,9,15]. Rather than representing a strategy to maximize their instantaneous speed, Bulwer's petrels use crosswinds to maximize the distance covered along their entire round trips from central places carried out in predictably stable wind fields. This anemotactic strategy is different than, for instance, that of gadfly petrels (e.g. Desertas petrels, *Pterodroma deserta*), which design fast long tracks consistently selecting a wind Δangle that enable them to maximize their instantaneous speed [6]. Compared to the larger gadfly petrels, Bulwer's petrels are smaller, fly at a lower ground speed and have lower wing loading and aspect ratio [14]. These anatomical features make headwind flight particularly disadvantageous [14] and potentially unsustainable and, in fact, the petrels only rarely engaged in headwind flight.

Tracked petrels also travelled beyond the trade winds belt, carrying out long clock-wise routes. Rather than commuting to distant foraging hotspots, we argue that the benefit of such longer trips may be the greater distance covered to increase the probability of encountering food en route. In line with previous evidence [33], we found that the Bulwer's petrel foraging range was not correlated with the temporal duration of their journeys owing to the higher average speed along the distant trips than along the near trips, underpinned by the use of comparably more advantageous wind Δangles. By exploiting higher variability in winds, petrels consistently chose more favorable Δangles and received more assistance from the wind (i.e. higher TWC) along the distant trips, resulting in the longer commutes being significantly faster than the respective simulated trajectories.

All these findings strongly suggest that Bulwer's petrels rely on an impressive knowledge of the regional wind availability and real time wind fields. When birds stay within the stable and more predictable trade winds region, they use crosswinds to cover as much distance as possible along the entire route, a strategy that will prevent them from performing long headwind commutes on the way back. Such selection for integrated optimization over the course of multi-day return route from a central place suggests that, upon departure, these animals may plan their overall route across that entire period, and anticipate the expected winds that they will experience days later when they return to the colony.

Crosswind flight and area scanned by olfaction

In line with previous evidence [17], we found that crosswind flight enables the birds to maximize the olfactory bandwidth, supporting H2. In fact, at low wind intensities, crosswind flight (i.e. Δangle values ~ 90°) maximized both the olfactory bandwidth and the theoretical area scanned. However, for higher wind intensities, the use of quartering-tailwinds results in a gain in speed and therefore in the area scanned per unit time that offsets the loss incurred from the smaller instantaneous range of detection of odour plumes (compared to the larger olfactory bandwidth achievable with crosswind). Our model highlights that the result of this trade-off varies with wind speed, but under most conditions faced by the petrels (the typical wind intensity in the study area is ~ 7 ms^{-1}), the theoretical predictions on area scanned per unit time are qualitatively similar (greater overall area scanned for wind Δangle smaller than 90°, between 60° and 65°). These values are smaller than the preferred Δangle (ca. 90°) most intensely used by the petrels along their tracks. Yet, despite this discrepancy, the overall roundtrip trajectories realized by the birds allowed for a significantly larger area scanned using olfaction than their respective simulated ones. Hence, rather than maximizing the area scanned at any given point in the foraging trip, our results suggest that the extensive use of crosswinds enables these birds to maximize the area scanned along their entire central place foraging trip routes.

Our findings strongly support the hypothesis that Bulwer's petrels search for foraging opportunities using their sense of smell, both during day and night, relying on crosswind flight to detect olfactory cues and opportunistically find prey along their route. This may

be the key to the ecological success of many other small petrels with similar foraging ecologies, which have global distributions and some of the largest seabird populations on earth. We found that petrels are highly selective of crosswinds not only when realizing fast transit movements, but also when searching for food, consistently for the finer-scale and coarser resolution datasets. Moreover, the petrels exhibit a strikingly similar distribution of wind Δangle both during day (when visual cues could be used more extensively) and night (when they are more visually limited). Had visual cues been used to detect prey, it would be reasonable to expect the foraging strategies and the movement behavior of petrels to differ considerably between night and day. Further evidence is also provided by the fine-scale movements documented in the 3-min tracks. In some sections, the birds seem to fly crosswind to detect odor plumes, track the smell upwind to the source upon detection, stop to forage, and then resume flying along the initial direction (fig. 5).

Zig-zag

An emerging property of the Bulwer's petrel tracks is a systematic crosswind zig-zag flight. This zig-zag flight occurs both at the large scale (1-h resolution), when the birds are carrying out fast transit movements, and at a smaller scale (3-min resolution), when they are performing ARS movements upon reaching areas offering good feeding opportunities (fig. 2). The 3-min dataset comprises large sections in which the petrels maintain constant heading, realizing straight crosswind tracks often for the whole duration of the recorded movement burst. Along some tracks, the birds performed sharp turns, changing heading by ~ 180° to fly in the direction from which they were coming. The extensive use of this crosswind zig-zag flight, and its potential importance as an efficient search strategy, is documented here for the first time.

Various anecdotal evidence from at-sea observations and both theoretical [8] and empirical studies [12] suggested that dynamic soaring albatrosses can fly without flapping their wings at virtually any angle with respect to the wind, including directly upwind, by "tacking" like a sail-boat. However, this implies several sections with an overall upwind heading and tacking manoeuvres with smaller turning angles compared to the sharp turns exhibited by the zig-zagging Bulwer's petrels. Furthermore, as we discussed above, the Bulwer's petrels very rarely engaged in upwind flight and are predicted to attain the lowest ground speed in such conditions. In fact, due to their wing morphology [14], sustained headwind flight may be particularly disadvantageous for Bulwer's and other small petrels. Hence, we argue that the systematic zig-zag undertaken by the petrels is underpinned by high selectivity for crosswind during the entire roundtrip, both to maximize the distance travelled and the area scanned olfactorily for foraging opportunities.

Conclusion

Under constant winds, Bulwer's petrels maximize the distance covered and the area scanned using olfaction by performing a systematic crosswind zig-zag flight. When conditions are suitable, petrels also undertake larger clock-wise looping routes, efficiently

designed to exploit the higher wind variability beyond the trade winds belt. The results of this study provide novel elements shedding further light into adaptations of dynamic soaring seabirds for the efficient use of stable and predictable winds. Such ecological features make seabirds particularly sensitive to the effects of climate change on the ocean winds. The general atmospheric circulation and particularly the intra-seasonal variability in wind conditions in the subtropics are predicted to be highly impacted by climate change [46,47]. In this context, a thorough understanding of the role played by wind in movement ecology of seabirds is pivotal, with direct implications for conservation and evidence-based management.

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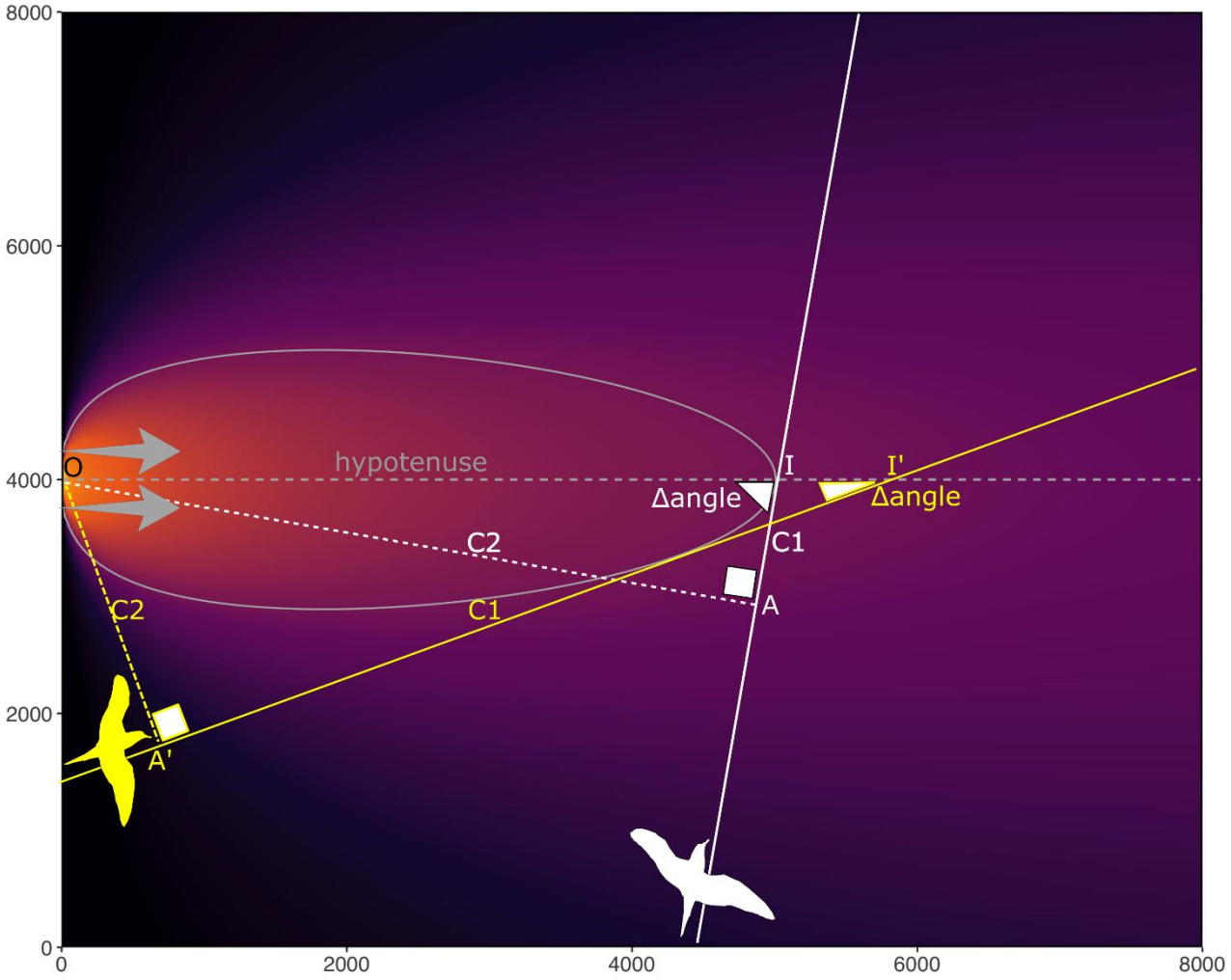
Tables and figures

Table 1. The median and interquartile ranges of wind direction relative to the bird bearing ("Δangle") quantified for the different track sections and temporal resolution.

Trip Section (resolution)	Δangle, median	Δangle, 25%–75% interquartile range
Overall (3-min)	85.30°	65.96°–101.04°
In flight (3-min)	89.90°	77.94°–103.36°
Mixed (3-min)	85.85°	72.58°–100.39°
On water (3-min)	52.19°	22.99°– 92.45°
Day (3-min)	85.42°	65.54°–101.67°
Night (3-min)	84.80°	67.74°– 98.73°
Overall (1-h)	80.03°	58.92°– 96.35°
Transit (1-h)	79.04°	60.33°– 92.71°
Search (1-h)	81.16°	57.67°–100.01°
Day (1-h)	80.14°	57.91°– 97.33°
Night (1-h)	79.85°	61.36°– 94.31°
Nearby (1-h)	88.81°	76.95°–104.64°
Distant (1-h)	72.02°	49.07°– 88.81°



583

584 **Figure 1.** The smell detection contour generated by the "odor plume model". The constant and
585 uniform wind is represented by the central arrows. The smell source is at "O". The x and y axes are
586 expressed in meters. Two potential trajectories are depicted, with birds flying at two Δangle
587 values: 10° and 80° (coloured and white solid lines, respectively). Two right triangles are obtained,
588 delimited by: the hypotenuse (OI' and OI for Δangle of 10° and 80° respectively); the cathetus "C1"
589 adjacent to Δangle (A'I' and AI, adjacent to the Δangle of 10° and 80°); and the cathetus "C2"
590 opposite to Δangle (OA' and OA). C2, calculated as C2 = hypotenuse * Sin(Δangle), is the "olfactory
591 bandwidth", i.e. the maximum distance from the source at which a smell can be detected.

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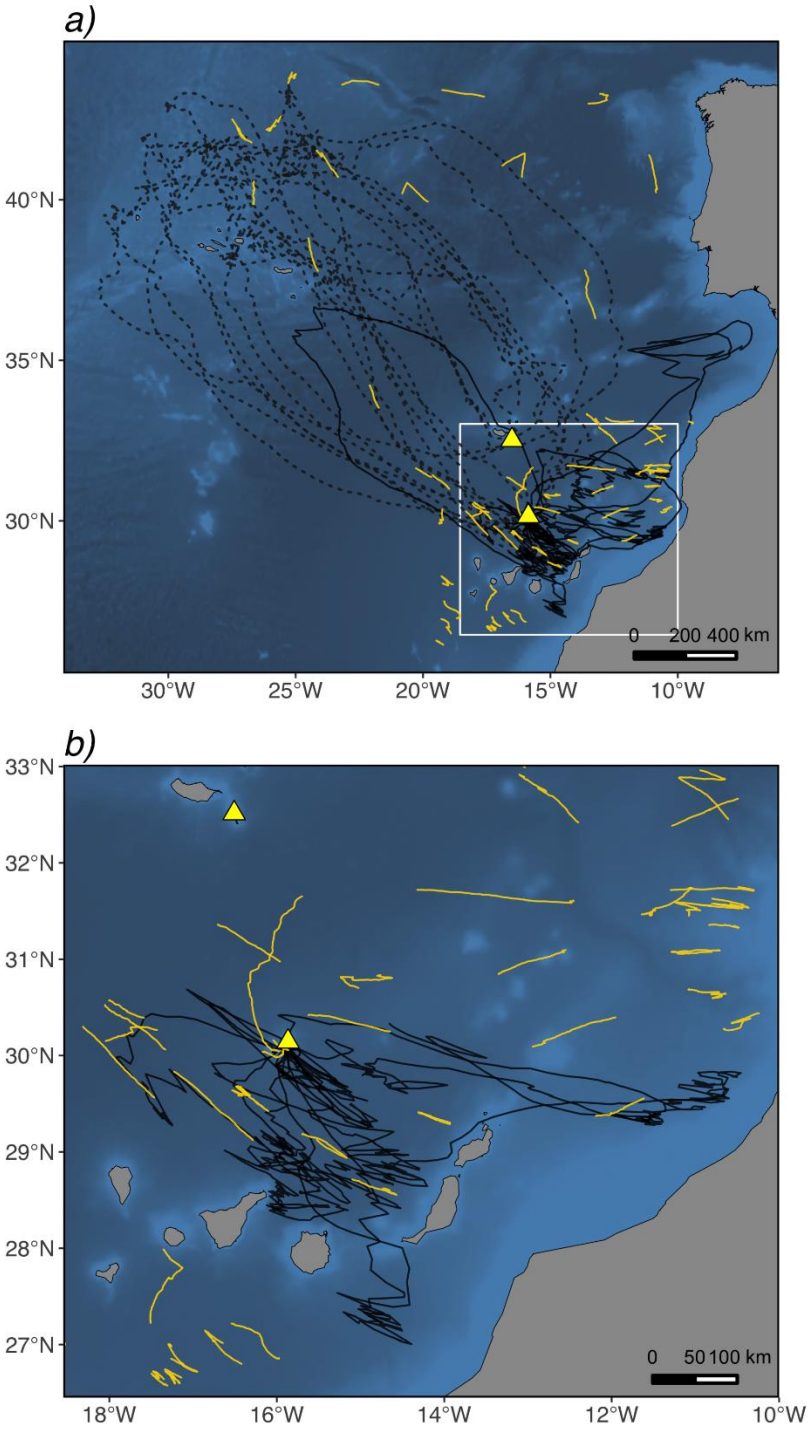


Figure 2. (a) All tracks, both at 3-min (in gold) and at 1-h resolution (in black) are depicted. The "distant" and "nearby" 1-h resolution trips are represented using dotted and solid lines, respectively. The inset map depicts the extent of panel (b) below. (b) A selection of 1-h and 3-min resolution tracks (in black and gold, respectively), highlighting the zig-zag flight performed by the petrels. The triangles indicate colony locations.

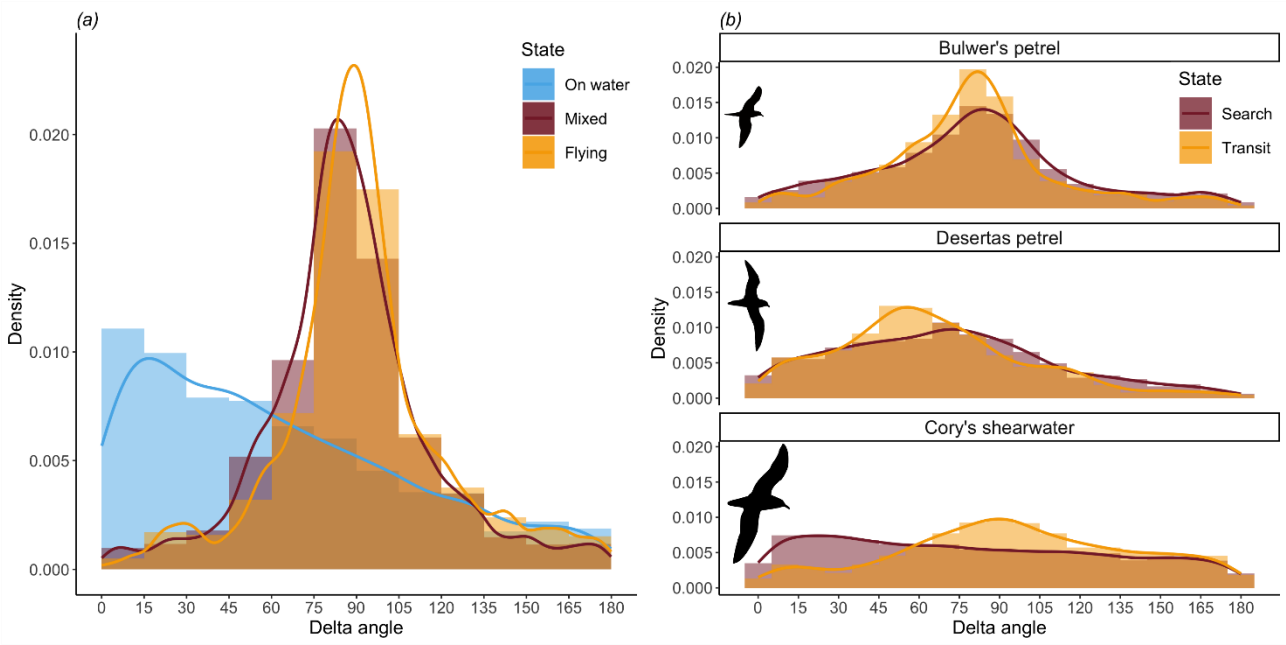
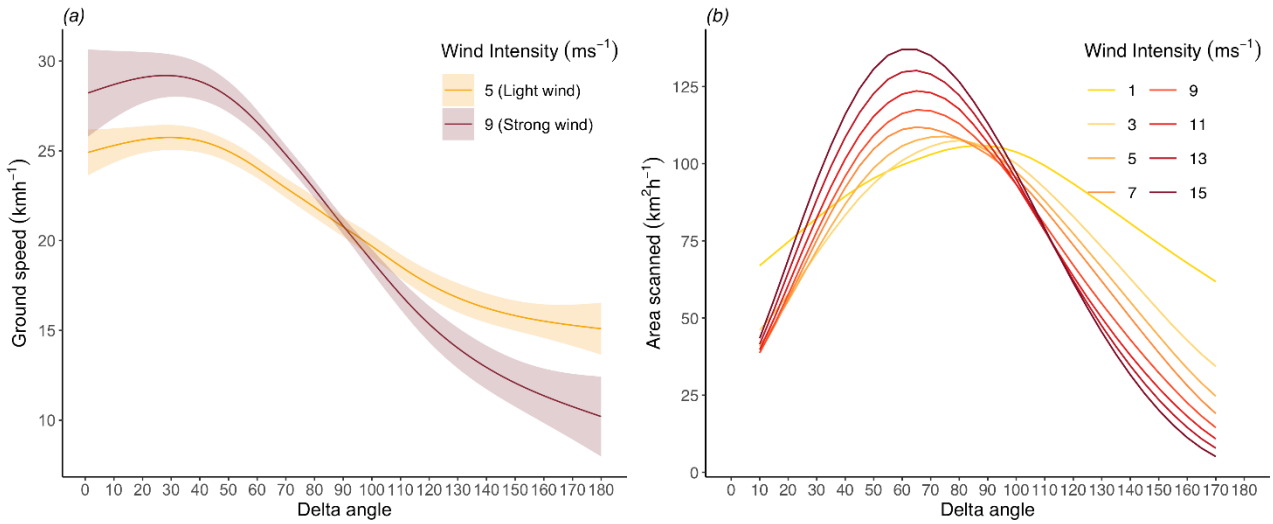


Figure 3. (a) Density curves of Δangle used by the Bulwer's petrels along the 3 min resolution tracks. Different colors are used to represent the different behavioral states. (b) The Δangle used by Bulwer's petrels along the 1-h resolution tracks during "search" and "transit" (in the top panel) is compared with that used by Desertas petrels (n = 25 tracks) and Cory's shearwaters (n = 103 tracks).



610

611 **Figure 4.** (a) GAMM "wind model", fitted to the transit segments of the 1-h resolution trips. The
612 95% confidence interval is represented by the shaded areas. For visualization purpose, the
613 predicted effect of Δangle on ground speed (kmh^{-1}) was calculated for light (5 ms^{-1}) and strong (9
614 ms^{-1}) winds. (b) The theoretical area olfactorily scanned (km^2 in 1 hour), as a function of wind
615 Δangle and wind intensity.

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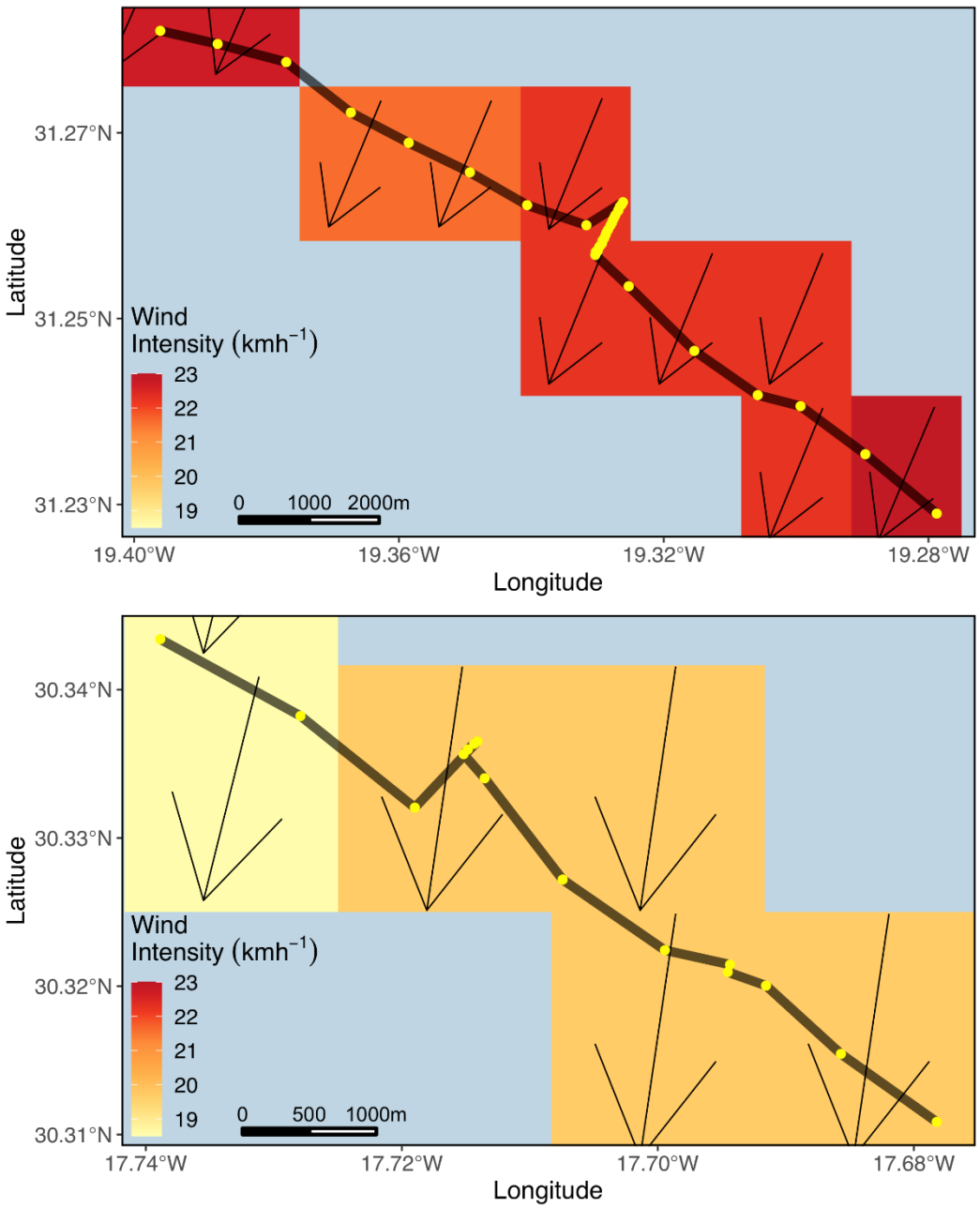

618

619 **Figure 5.** Two examples indicative of the occurrence of olfactory foraging along the 3-min
620 resolution tracks. In both examples, the petrels fly crosswind, at night, moving from northwest to
621 southeast. In two sections of the movement bouts (one per panel), the birds seem to: track the odor
622 plume upwind for approximately 500 m; engage in foraging; sit on the surface of the water to
623 process food (indicated by the sections in which the points are clustered together); finally, resume
624 flying along the initial direction of movement. The arrows represent the real-time wind conditions
625 experienced along the tracks, whereas the yellow points are the GPS locations.