Fine-scale movement data of the endangered Bermuda petrel highlights surface foraging and greater nocturnal flight activity.

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Abstract

Foraging behavior plays a fundamental role in animal fitness and population dynamics, particularly in marine ecosystems where seabirds like petrels showcase a diverse array of foraging strategies finely adapted to the pelagic environment, but rarely studied. However, the extent and remote nature of their foraging grounds makes direct observation of foraging behaviour impractical, thereby requiring the use of remote tracking technology. We deployed miniaturized multi-sensor biologgers and collected fine scale movement data to investigate the at-sea behaviours of the Bermuda petrel *Pterodroma cahow*, a poorly studied and highly threatened gadfly petrel, specialised on mesopelagic prey. GPS-tracking data revealed extensive foraging trips, in consistent directions, over remote oceanic regions. Accelerometer-data analysis highlighted three flying-related and three water-related behaviours. Flying behaviour reflected the expected dynamic soaring flight strategy of procellariforms; individuals spent more than three-quarters of their time in flight with non-flapping flight being the most common behaviour under all conditions. A third and less frequent flight behaviour: the intensive flight, could indicate "aerial dipping", a characteristic foraging technique of Pterodroma species. The remaining time was spent in three water behaviours: active, inactive, and intensive, with the latter being less common but likely reflecting scavenging and prey seizing. All behaviours but intensive water and flight had a diel activity pattern. Flight-related behaviours increased with negative sun elevation values while water-related behaviours showed an opposite trend, highlighting greater flight activity during nighttime. Finally, time-depth-recorders complemented the results suggesting that the meso-bathypelagic prey targeted by petrels must be available in the very upper layer of the water surface, given the very limited diving capacity of petrels. While some of our findings may require further validation to confirm their relevance to foraging behaviour, our work offers new insights to take into consideration when assessing the extent and nature of offshore anthropogenic-related risks faced by petrels.

Introduction

Foraging is a crucial component of animal behaviour with direct implications for individual fitness, survival and population demography [1]. In marine ecosystems, foraging behaviour establishes a predator-prey link influencing both the trophic connectivity and the carbon flux in the oceans [2,3]. Identifying a predator's at-sea behaviour and foraging strategy is beneficial for understanding the species' ecological requirements and roles in ecosystems. Procellariiform seabirds such as petrels and albatrosses are upper-level predators of pelagic food webs showing an impressive range of foraging strategies and feeding techniques [4]. They are well adapted to perform long-distance dynamic soaring flight with minimal energy expenditure [5], enabling them to spend a significant portion of their life in the open ocean while in search of food resources.

The only way to study pelagic seabirds' at-sea behaviour is through the use of miniaturized biologgers that collect data on different aspects of their movements and foraging behaviour [6, 7], alongside the biophysical conditions they encounter at sea [8]. Despite recent advances in biologging techniques, some of these aspects including flight behaviour, activity pattern and feeding techniques of many small- and medium-sized seabirds, such as petrels, remain poorly understood [9]. Until recently, the foraging behaviour of petrels and other seabirds was mainly ascertained through knowledge of the ecology of prey found in their stomachs and regurgitates [10–12]. Though this method has contributed to a better understanding of the ecological role of petrels and other seabird in food webs, it also produced contrasting result. For example, when comparing mesopelagic prey biology (migrating vertically at night) with greater diurnal predator activity derived by data-loggers [13].

Gadfly petrels of the genus *Pterodroma* are pelagic seabirds morphologically and anatomically designed to exploit wind energy to perform prolonged and efficient dynamic soaring flights [14] during which they mostly glide on the ocean surface with limited flapping-flight [15]. The species within this group are also ecologically very similar, with a diet based predominantly on deep sea mesopelagic prey [16, 17] that they capture using different feeding techniques [18]. Indeed, *Pterodroma* petrels are believed to forage while in flight by contact "dipping" to the surface (or "stooping"/"aerial dipping", that is, taking up prey in flight while barely touching the sea surface) [19] which is considered a shared trait among congeners [20]. Similarly, they may also feed while sitting on the water through surface-seizing or scavenging, and less frequently, by searching for prey underwater [21, 22]. Because of their mesopelagic-prey specialization, including mainly fish (mostly Myctophids) and cephalopods [17] that are available by means of diel vertical migration [23], petrels are also expected to forage at night [10, 17, 18], thus supporting the idea of a marked nocturnality [10, 18, 24]. Furthermore, because of their morphology (e.g., body size, long wing, lack of laterally compressed legs) and physiological characteristics, *Pterodroma* petrels are not regarded as proficient divers unlike shearwaters or diving-petrels [15, 19, 22, 25–27] (see references in [28]). However, the diving capacity and performance in this genus are still anecdotic or poorly investigated.

In the present study we investigated the at-sea behaviour of the Bermuda petrel (*Pterodroma cahow*), a globally endangered gadfly petrel endemic to the western North Atlantic that breeds exclusively in the Bermuda Islands [29, 30]. To date, only two studies have investigated the marine distribution and foraging ecology of the Bermuda petrel during the breeding season [16, 31]. The ecological insights they provide indicate that *P. cahow* flight, similarly to other congeners, can be modulated through wind selection, likely facilitating extended and prolonged foraging trips [16] while minimizing energy expenditure. Although the diet of the Bermuda petrel is dominated by meso- and bathypelagic fish (mostly Myctophids) and cephalopods [16], which would indicate substantial nocturnal foraging activity, a previous analysis of GPS-data suggested an equivalent amount of "searching" behaviour (i.e., putative foraging) vs "transit" by day and night [16]. The mismatch between diet and GPS data and the lack of knowledge of the species' daily activity pattern cast substantial doubts on its presumed nocturnality. With the aim of reconciling these discrepancies and improving our understanding of unknown aspects of Bermuda petrel behaviour at sea, we combined the use of GPS, tri-axial accelerometer, and temperature-pressure sensors to collect complementary and high-resolution information that we used to (i) characterise petrels' foraging areas, (ii) identify behavioural modes when they are in flight and on the water including diving activity, and (iii) test whether and how these behaviours change in relation to light-to-dark conditions.

Materials and Methods

Biologging data collection

Biologging devices were deployed on 25 incubating Bermuda petrels at Nonsuch Island, Bermuda (32.347°N, 64.663°W) between 22 January and 9 February 2023. Birds were temporarily equipped with loggers on their backs or tails using Tesa tape 4651. Most loggers were recovered 13-26 days later. Three logger types were used in this study: Axy5 loggers (Technosmart, Italy, 2.5 g) that included tri-axial accelerometers (25 Hz), tri-axial magnetometers (1 Hz), and temperature-pressure sensors (1 Hz), were deployed on the backs of 9 petrels; AxyTrek loggers (Technosmart, Italy, 5 g) that included GPS sensors (5 min), tri-axial accelerometers (25 Hz), and temperature-pressure sensors (1 Hz) were deployed on the backs of 5 petrels; and Nano-fix GEO loggers (PathTrack, United Kingdom, 3.4 g) that only recorded GPS locations (1 hr) were deployed on the tail of 11 petrels (see for details on attachment method [16]). Birds' body weight ranged between 300 and 385 g (N = 25); thus, the heavier loggers (AxyTrek) corresponded to

1.3-1.7% of body mass while the lighter loggers (Axy5) corresponded to 0.8-0.65% of body mass, respectively. Data from deployments and biologgers are included in Table 1. Field work procedures were approved by the Department of Environment and Natural Resources (DENR), Government of Bermuda, and by Ispa Ethical Committee for Animal Welfare (ORBEA) and carried out under licence (nos. 19-12-04-87 and 22-12-06-112) issued by DENR.

					Total Track			Foraging Trip					
Colony	Tag type	Nest	Bird	Sex	Start	End	Duration (days)	Trip	Start	End	Duration (days)	Maximum distance (km)	Notes
A	Axy5	R819	E0368	M	2023-01-25 20:27	2023-02-03 1:03	8.2	1	2023-01-26 9:20	2023-01-31 1:35	4.7		Complete
	PathTrack	R820	E0487	F	2023-02-02 2:07	2023-02-17 18:07	15.7	1	2023-02-08 2:07	2023-02-17 6:07	9.2	1493	Complete
	PathTrack	R820	E0243	M	2023-01-23 2:03	2023-02-08 3:04	16.0	1	2023-01-26 11:03	2023-02-07 22:04	12.5	1503	Complete
	Axy5	R821	E0362	M	2023-01-23 0:00	2023-01-31 3:28	8.1	1	2023-01-24 6:20	2023-01-27 3:35	2.9		Complete
	PathTrack	R834	E0161	F	2023-01-29 2:00	2023-02-12 19:00	14.7	1	2023-02-01 6:00	2023-02-11 2:00	9.8	1100	Complete
	Axy5	R834	E0182	M	2023-01-25 21:07	2023-02-03 5:37	8.4						In burrow
	AxyTrek	R835	E0220	M	2023-01-26 0:00	2023-02-02 8:03	7.3	1	2023-02-01 7:35	2023-02-02 8:05	1.0	[549]	Incomplete
	Axy5	R836	E0401	F	2023-01-25 20:15	2023-02-03 3:52	8.3						In burrow
	AxyTrek	R836	E0171	M	2023-02-09 0:00	2023-02-18 22:01	9.9	1	2023-02-18 2:55	2023-02-18 22:00	0.8	[1075]	Incomplete
	PathTrack	R837	E0801	F	2023-01-29 2:02	2023-04-01 14:06	62.5	1	2023-01-30 8:02	2023-02-01 6:02	1.9	232	Complete
								2	2023-02-11 7:02	2023-02-23 23:05	12.7	1433	Complete
	PathTrack	R839	E0363	F	2023-01-26 2:03	2023-02-19 19:05	24.7	1	2023-02-04 5:02	2023-02-18 2:05	13.9	1003	Complete
	PathTrack	R840	E0484	M	2023-01-26 2:02	2023-02-08 3:02	13.0	1	2023-01-28 5:01	2023-02-03 3:02	5.9	675	Complete
B	AxyTrek	B12	C0888	F	2023-02-10 0:00	2023-02-18 7:33	8.3	1	2023-02-18 1:55	2023-02-18 7:35	0.2	[231]	Incomplete
	Axy5	B12	E0252	M	2023-01-26 21:10	2023-02-04 4:47	8.3						In burrow
	Axy5	B2	C0901	M	2023-01-26 20:00	2023-02-04 4:04	8.3	1	2023-01-27 6:35	2023-02-03 4:05	6.9		Complete
	Axy5	B8	E0083	F	2023-02-10 0:00	2023-02-18 2:18	8.1	1	2023-02-10 0:00	2023-02-18 2:20	8.1		Incomplete
	Axy5	B8	C1036	M	2023-01-26 21:00	2023-02-03 17:59	7.9	1	2023-01-28 7:15	2023-02-03 18:00	6.4		Incomplete
	PathTrack	B9	E0552	F	2023-01-27 2:00	2023-02-14 23:00	18.9	1	2023-02-07 1:00	2023-02-14 23:00	7.9	1241	Complete

Table 1. Summary of tracking data and foraging trips of Bermuda petrels tracked from Nonsuch Island in 2023.

Defining foraging trips and at-sea distribution using data from birds tagged with GPS-loggers

We defined foraging trips as any period when the bird was more than 1 km from the colony. Only complete tracks were taken into account and used to calculate the maximum distance from the colony and the overall temporal duration of the trip. Afterward, we fitted discrete-time Hidden Markov models (HMMs) to the data using the package moveHMM [32] in R [33]. We used 2-state HMMs to classify the behavioural states of the birds along the tracks based on the distance travelled (step length) and the change of movement direction (turning angle) observed at each movement step. The most likely sequence of behavioural states was inferred using the Viterbi algorithm [34]. We assumed that, along the tracks, the birds were in one of the following behavioural states: 'transit', in which birds were moving at high speed at a persistent heading; or 'search', in which birds were performing convoluted movements at a comparatively lower speed [35, 36]. We considered the search behaviour state to be associated with food searching or putative foraging behaviour, although it can also include resting behaviour (for more details see [16]). Furthermore, we estimated the direction of both outbound and inbound trips. To do so we calculated the mean angle direction of the first burst of tracking locations labelled as 'transit' exiting the colony within a range of 400 km from the colony. The inbound direction was estimated as the mean direction of the last burst of tracking locations labelled as 'transit', meaning the end of their persistent travel back to the colony. Finally, we fitted a continuous-time movement model to calculate a population-level utilization distribution (UD) of foraging areas using 95, 75, 50 and

25% autocorrelated kernel density estimate (AKDE) for all the individuals using the functions `akde` and `pkde` from the package `ctmm` [37, 38]. We fitted the AKDE with all tracking data and only with the data labelled as 'searching' by the HMM excluding locations in the 50 km radius of the colony (see [16]).

Diving Activity

Depth data were collected at 1 Hz with a resolution of 0.005 m. Two outliers with depths greater than 15 m were removed from the dataset (<0.00003% of all depth measurements) and these missing values were replaced with linearly interpolated values. A zero-offset correction (ZOC) was calculated based on the 10th percentile of depth over a 10-minute moving window. ZOC ranged from 0 -0.49m. The ZOC was subtracted from all depth measurements and corrected values <0 m were fixed at 0 m. We examined histograms of depth measurements while birds were engaged in foraging trips (see the following section for details of behavioural classification) for evidence of diving activity.

Accelerometer-derived movement metrics

We calculated a range of accelerometer-derived metrics shown to be useful in characterizing bird behaviour and different modes of flight [39–42]: surge acceleration, sway acceleration, heave acceleration, dynamic surge acceleration, dynamic sway acceleration, dynamic heave acceleration, body pitch, body roll, vectorial static body acceleration (VeSBA), vectorial dynamic body acceleration (VeDBA), and wingbeats. VeDBA and VeSBA were calculated following [42]. VeSBA measures gravitational acceleration which should be close to 1 when the animal is stationary or making linear movements, and greater than 1 when the bird is turning [42]. VeDBA measures total dynamic movement of the animal, which can be influenced by intrinsic movements and environmental conditions [42]. All measures except wingbeats were calculated over a 1-sec moving window. Wingbeats were identified using the `findpeaks` function in the `pracma` package (version 2.4.2 [43]). Potential wingbeats were first identified as peaks in heave acceleration with an amplitude >1g where at least 2 successive peaks occurred within 4 Hz.

Behaviour classification

We used a supervised machine learning approach to identify consistent behaviours from the accelerometer tracking data. First, we visually examined plots of the accelerometer derived metrics at different time scales (e.g. 15 sec, 1 min, 5 min, 1 hour) to identify consistent patterns that were likely associated with nine general behaviours: 3 behaviours in the burrow, 3 behaviours associated with swimming, and 3 flight behaviours. From visual examination of the accelerometer-derived measures (previous section), we found that acceleration in the heave axis, pitch, roll, VeSBA, VeDBA, and temperature were most useful in visually identifying characteristic behaviours that are likely associated with the burrow, flying, and swimming. Table 2 provides a description of the characteristics of the nine behaviour classes. We randomly selected 400 15-sec segments from each bird tracked with an accelerometer (n = 4400 segments). Each segment was manually classified to one of nine possible behaviours by a single observer (AP). Segments were each classified twice in random order. Segments that were not classified consistently to the same behaviour were reviewed a third time to determine a final classification. Training data were split into training and validation data sets, with half of the segments for each behaviour class randomly assigned to training or validation. For each 15 sec segment in the tracking data, we calculated summary statistics of the 12 accelerometer metrics described previously. Summary statistics included mean, inter-quartile range (IQR), 10th quantile, 90th quantile, and sum (only applied to wingbeats); a detailed explanation of how each metric was summarized is provided in Table S1. This resulted in 36 potential predictor variables for behavioural classification. We used the training data to fit a classification algorithm for the nine behavioural states. Behavioural classification was conducted using random forest models with the `ranger` package (version 0.16.0 [44]), model training and selection was done using `caret` package (version 6.0-94 [45]) in `R`. Model tuning was done using repeated k-fold cross validation with 5 repeats of 10 folds, within each fold 50% of the data were withheld for model testing. Behavioural classes were up-sampled to ensure even sample sizes across all behaviours within the training dataset. Model tuning parameters were selected using a random search with different values for the hyperparameters of minimum node size (min.node.size), number of variables used at each node (mtry), and splitting rule. A final model was fit to the full training dataset using the hyper-parameters with the highest Kappa value.

Behaviour	Behaviour characteristics	Training segments
Burrow - still	Consistent high temperature; low VeDBA; virtually no variation in surge, sway, and heave axes	1350
Burrow - stirring	Consistent high temperature; low VeDBA with max VeDBA < 1 g; small amplitude variations in surge, sway, and heave axes	715
Burrow - active	Consistent high temperature; max VeDBA > 1 g; sustained variation in VeDBA, surge, sway, and heave axes; changes in pitch and roll greater than 10°	338
Flying - non-flapping	Consistent fluctuations in VeSBA with peaks > 1.5 g; consistent low frequency fluctuations in heave acceleration with peaks > 2 g; absence of wing beats	102
Flying - flap-glide	Consistent fluctuations in VeSBA with peaks > 1.5 g; consistent fluctuations in heave acceleration with peaks > 2 g; at least one bout of 3 successive wing beats	540
Flying - intensive	Fluctuations in VeSBA with peaks > 1.5 g; luctuations in heave acceleration with peaks > 2 g; sustained bouts of wing beats > 4 sec, unusually high amplitude wingbeats (>2 g); irregular variation in pith or roll	70
Water - inactive	Low mean and peak VeDBA; random low amplitude variation in VeDBA, surge, sway, and heave acceleration; minimal variation in VeSBA	88
Water - active	Mean VeDBA > 0.1 g and < 1 g; non-random variation in surge, sway, and heave acceleration; fluctuations in pitch or roll >10° and <50°; minimal variation in VeSBA	130
Water - intensive	Low variation in VeSBA, peak VeSBA <1.5 g; high mean VeDBA > 1g, peak VeDBA > 2g; large variation in pitch/roll > 50°; intense non-random variation in surge, sway, and heave acceleration	116

Table 2. Description of the movement characteristics used to manually classify training segments to nine behaviour classes. Final column shows the number of randomly selected segments classified to each behaviours. Although 4400 random segments were initially selected, 26 segments could not be reliable assigned to a behaviour class and were removed from the training dataset.

We compared three sets of models using different combinations of predictor variables (Table S1) (Full model) all 36 accelerometers variables, (Correlation model) a subset of variables with correlations < 0.7, and a subset of variables with the highest variable importance identified through recursive feature elimination (RFE model [45]). Table S1 indicates which variables were included in each of the three model sets. We compared the resampled Kappa statistics for these three models to identify the best model for behavioural classification. Kappa for the Full model (mean = 0.84, range = 0.83-0.85) and the RFE model (mean = 0.83, range = 0.82-0.85) were similar, therefore we selected the simpler RFE model for the final behavioural classification. We used the RFE model to predict behavioural classifications to all segments. The withheld validation segments were used to estimate the accuracy of the final model on independent data. We examined the overall classification accuracy and Kappa. We explored the behaviour specific classification accuracy by looking at balanced accuracy for each of the nine behaviours and for the three behavioural modes (burrow, water, flying). We looked at the variable importance measures to determine which accelerometer measures contributed the most to classification accuracy.

Daily activity patterns

We calculated the proportion of time spent in the six at-sea behaviours over 1-hour intervals (from 8 birds, hereafter accelerometer-derived behaviours), and the proportion of time spent in the two at-sea states over 4-hour intervals (from 7 birds, hereafter GPS-derived behaviours) and estimated the sun angle (in radians) for each time step using the coordinates of the colony [46]. For each behaviour we fit a zero-inflated beta generalized linear mixed models with sun angle as a fixed effect, random slope and intercepts for bird identity, and a first order autoregressive correlation structure [47]. We generated posterior predictive plots to check for systematic discrepancies between model output and the observed data [48].

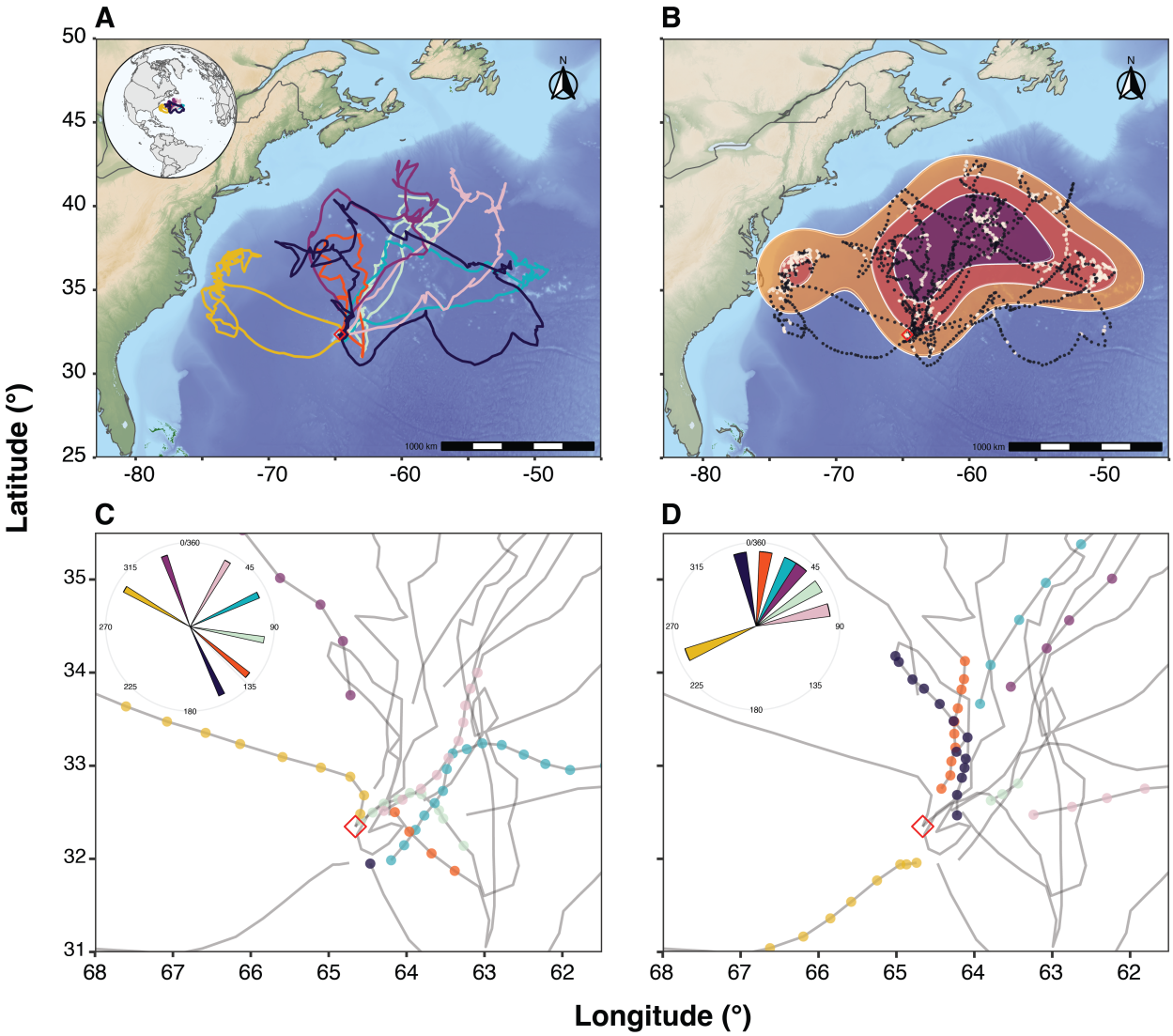

Figure 1. A) Foraging tracks for seven Bermuda petrels tracked from Nonsuch Island, Bermuda during incubation in 2023. Tracks show seven complete foraging trips recorded using PathTrack Nano-Fix GPS units; B) UD 95,75,50 and 25% calculated using only "search" classified location through HMM (white dots); C) Inbound directions calculated for the 8 foraging trips shown in A; D) Outbound directions of the same foraging trips.

Results

Tracking summary

Tracking data were obtained from 60% of the AxyTrek deployments (3 of 5), 89% of the Axy5 deployments (8 of 9), and 63% of the PathTrack deployments (7 of 11). The AxyTrek and Axy5 devices lasted for a mean of 8.3 days (see Table 1). Loggers with GPS sensors (PathTrack units) recorded eight complete foraging trips from seven petrels (Fig. 1), and three incomplete foraging trips from three petrels (AxyTrek units, Fig. 2). Loggers with accelerometers (Axy5 and AxyTrek) recorded 3 complete foraging trips and 5 partial foraging trips; three petrels with Axy5 devices remained in their burrows through the entire deployment.

Foraging trips and at-sea distribution calculated using loggers with GPS sensor

During the study period, we recorded 7 complete incubating foraging trips from petrels tracked with GPS loggers (Pathtrack devices; Fig. 1A). The mean (± SD) duration of the trips was 10.3 ± 2.9 d with an average maximum distance travelled from the colony of 1207 ± 305 km (Table 1). The marine foraging distribution of petrels (including only locations classified as "search" by HMM) during the tracking period covered an area of 1,939,342 km2 (UD 75%). Two main core areas (UD 25%, 438,609 km^2) were identified, both overlapping with the high seas in the western North Atlantic (Fig. 1B). The first core area was located beyond the continental shelf of the Eastern USA coast and the other one, in the deep-sea water between Bermuda and the continental shelf of Nova Scotia and Newfoundland (Canada) (Fig. 1B). The angles of the inbound foraging trips were scattered between NW (300°) and SE (161°) (Fig. 1C). The outbound angles were mostly clustered between 345° and 80° (NW-E) with only one bird exiting the colony from South-West (243°) (Fig. 1D).

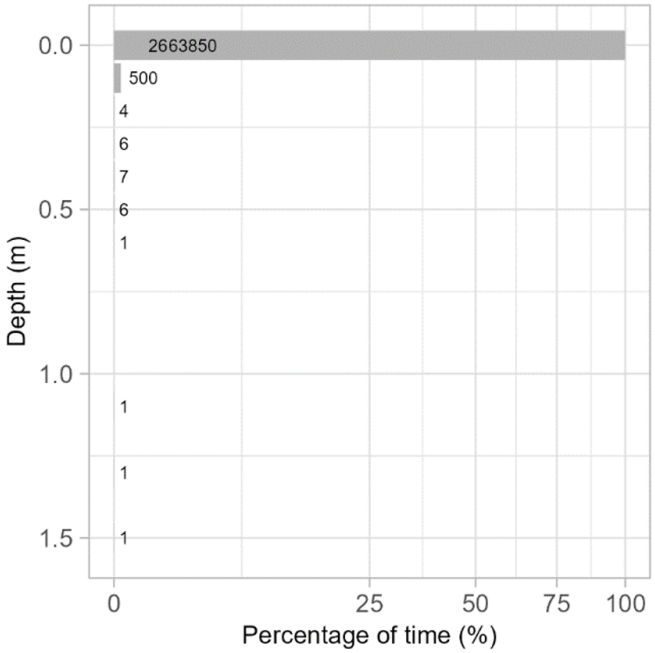

Figure 2. Percentage of depth measurements within 0.1 m depth classes, pooled across all foraging trips. Numbers to the right of bars represent the number of depth measurements in that depth class. The x-axis is square-root transformed to improve visualization of the range of values in the plot.

Diving behaviour

We found no evidence that petrels engaged in diving activity. After applying the ZOC to account for drift in the pressure sensor, less than 0.001% of observations from 8 petrels had depths greater than 0.1 m and the deepest depth recorded was 1.6 m (Fig. 2).

Accelerometer and behaviour classification

Overall, the random forest model predicted behaviours with 87.1% accuracy (CI: 85.7 – 88.5) with a Kappa of 83.9%. Most individual behaviours had balanced classification accuracy between 85.6% and 96.5%, except for the "flying-intensive" behaviour (61.7%, Table 3). When behaviours were further collapsed into three main modes of burrow, water, and flying, model accuracy increased to 98.7% (CI: 98.2 – 99.1), with a Kappa of 97.7% and balanced accuracy for individual classes between 96.3% and 99.6%. This shows that most misclassification of behaviours occurred within these three main behavioural modes. The five most important variables in the classification were

mean VeDBA (100%), the 90th quartile of VeDBA (82.3%), mean dynamic sway acceleration (78.8%), mean dynamic heave acceleration (76.1%) and the IQR of heave acceleration (74.4%, Fig. S1). Burrow behaviours had low measures of activity, relative to the other behaviour classes, across almost all accelerometer metrics and relatively high mean temperature (Fig. S2). Burrow-still had the lowest values across all measures of acceleration. Similarly, burrow-stirring had higher activity measures than burrow-still, but values were lower than for other behaviours. The burrow-active behaviour had similar mean VeDBA and mean dynamic surge to the water-inactive behaviour, however burrow-active had lower IQR heave acceleration and lower IQR VeSBA (Fig. S2).

Behaviour	Precision	Recall	Accuracy	Mode	Precision	Recall	Accuracy
Water - inactive	0.875	0.714	0.856	Water	0.936	0.931	0.963
Water - active	0.736	0.877	0.933				
Water - intensive	0.867	0.788	0.892				
Flying - intensive	0.529	0.237	0.617	Flying	0.982	0.989	0.989
Flying - flap-glide	0.868	0.890	0.936				
Flying - non-flapping	0.920	0.955	0.965				
Burrow - active	0.800	0.804	0.894	Burrow	0.998	0.994	0.996
Burrow - stirring	0.771	0.762	0.860				
Burrow - still	0.928	0.925	0.947				

Table 3. Behaviour specific performance metrics for the random forest model predicting Bermuda Petrel behaviour from accelerometer data. Left-hand columns show results for detailed behavioural classes and right-hand columns show results for general behavioural modes.

The three water behaviours were distinguished from the three flying behaviours by lower IQR in both the heave axis and VeSBA (Fig. S2). Water-inactive had very low VeDBA (Fig. S3) and likely represents periods of resting on the water when virtually all movement is coming from external motion on the water rather than motion of the bird. Water-active had higher activity overall than water-inactive, but still has low VeDBA compared to other at-sea behaviours (Fig. S2). The water-active class likely represents periods of minimal activity, for example when the bird is actively maintaining its position in the current through swimming. Water active could include passive foraging movements, like picking at prey at the surface, but not movements consistent with active pursuit of prey or competition with other birds Water-intensive had the highest activity measure of all the water behaviours, this was especially pronounced in mean VeDBA, wingbeats, and mean dynamic surge. High dynamic surge was likely associated with repeatedly dipping the head into or towards the water, potentially to catch prey or as part of bathing/preening (Fig. S3). The occurrence of sporadic wingbeats could also be associated with preening or short hops across the water.

The three flight behaviours were all characterised by high values of mean VeDBA, IQR heave, and IQR VeSBA (Fig. S2). Flap-glide flight and non-flapping flight had similar values for mean VeDBA, but flap-glide had higher numbers of wingbeats and lower IQR VeSBA. The large variation in VeSBA during non-flapping flight is consistent with petrels using dynamic soaring to reduce energetic costs under favourable wind conditions and using bouts of flapping to power flight when wind conditions do not favour dynamic soaring (Fig. S4). Intensive flight had more wingbeats per second than flap-glide flight, as well as more dynamic acceleration in the surge axis. Higher wingbeats could be associated with take-offs and landings or other aerial manoeuvring. Higher dynamic heave acceleration, like water-intensive, could indicate dipping or plunging toward the water. The classified intensive flight behaviour had much lower accuracy against the validation data then the other behaviour classes, it likely reflects a range of short duration that share the characteristics of unusually high wingbeats and high IQR in the VeSBA. As *Pterodroma* petrels are known to forage in flight [19, 20], it is plausible that all three flight behaviours could include foraging.

Activity Budgets

While on foraging trips, petrels spent more than three quarters of their time in flight (Fig. 3 and 4). Petrels spent almost twice as much of their time at sea in non-flapping flight (52.9 ± 14.5%, range: 26.8-67.1%) as in flapping

flight (27.6 ± 11.2%, range: 12.7-46.1%) (Fig. 3). Most of the remaining time was spent on the water, with similar proportions of trip time spent active (9.2 ± 1.5%, range: 7.3-10.8%) and inactive (6.2 ± 4.7%, range: 0.14-11.9%). Slightly less time was classified as water-intensive (4.5 ± 1.5%, range: 2.3-6.4%). Across all birds, only a small proportion of time was classified as flying-intensive (0.9% ± 0.6; 0.2-1.7%).

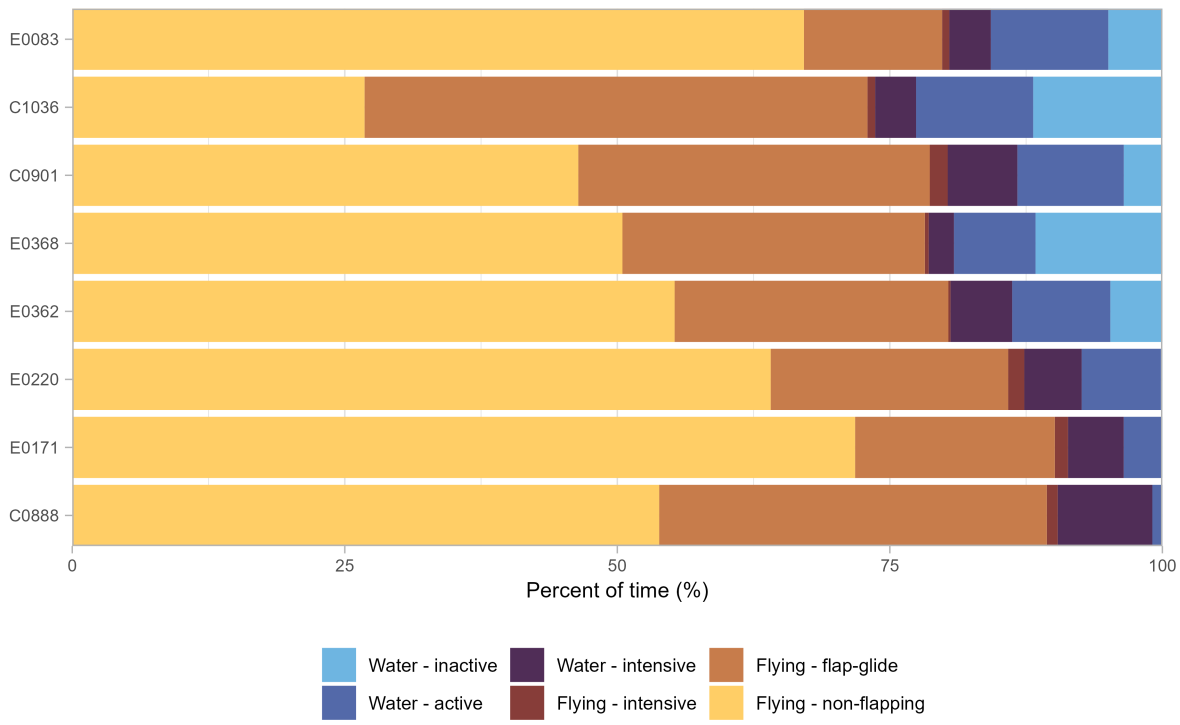

Figure 3. Activity budgets of the 8 Bermuda petrels tracked from Nonsuch Island with accelerometers in 2023. Colours indicate the six behaviours classified using a random forest model, individual bird identities are indicated on the y-axis.

Daily activity patterns

Sun angle influenced the proportion of time birds spent in all accelerometer-derived behaviours during foraging trips, except intensive flight (Fig. 5A-F and Table 4). Non-flapping flight was the most common behaviour under all conditions. Both non-flapping and flap-glide flight had high probability of occurring at all sun angles, but probability of occurrence declined with positive sun angles (Fig. 5E-F and Table 4). The proportion of time spent in flap-glide flight had a strong negative association with sun angle (Fig. 5E). All three behaviours on the water were positively associated with solar angle (Fig. 5A-C), increasing both in occurrence and proportion of time spent in the behaviour (Table 4). Interestingly, both the active water and water-intensive behaviours had a higher probability of occurring than the inactive water behaviour, but birds spent a lower proportion of time in these behaviours when they did occur. This likely reflects that resting occurred more sporadically but lasted longer than other surface activities. Sun angle had no relationship with intensive flight, which was the most uncommon behaviour under all conditions (Fig. 5D). Collectively, this demonstrates that Bermuda petrels are primarily aerial during the night and only spend significant time on the water during the day.

In addition, the probability of occurrence of the GPS-derived behavioural state "search" increased with the sun elevation, hence with higher probability during the day (Fig. 5G, Table 4), but the proportion of time spent searching which may include resting on water as well as putative foraging did not change between night and day (Fig. 5G, Table 4) and was stable on high proportions (75-80%). Whereas the probability of occurrence and the proportion of time spent in "transit" slightly decreased during the day, but still remained on higher values (62-85%) at all sun

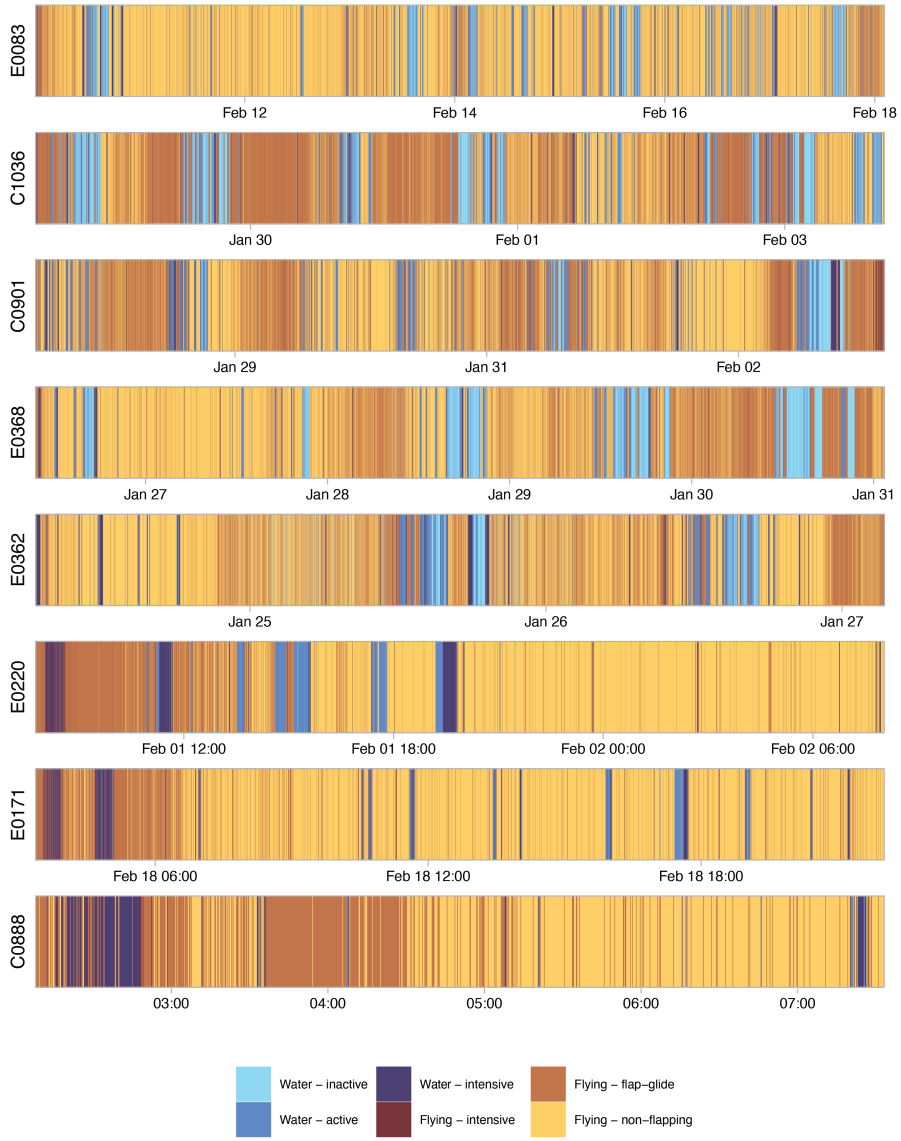

Figure 4. Sequence of classified behaviours within deployments of accelerometers on Bermuda petrels. Colours indicate the six behaviours classified using a random forest model, individual bird identities are indicated on the y-axis. Note that dates are different along the x-axis for each bird because deployments were not concurrent.

elevations (Fig. 5H, Table 4).

Discussion

We analysed movement data, activity patterns and diving behaviour to quantify fine scale at-sea behaviours of incubating Bermuda petrels. Similar to previous studies [16, 31], GPS tracking showed that Bermuda petrels undertook extended foraging trips to the NNE of Bermuda, apparently targeting the path of the Gulf Stream, and confirming a reliance on vast oceanic areas for successful foraging as in other *Pterodroma* petrels [14, 16, 49, 50]. However, in contrast to many other Procellariiformes [10, 27], which can perform dives of considerable duration and

Accelerometer-derived behaviours				
Behaviour	Zero-inflated model		Conditional model	
	Intercept	Sun angle	Intercept	Sun angle
Water - inactive	0.72 ± 0.09 ***	-1.26 ± 0.14 ***	-1.40 ± 0.14 ***	0.57 ± 0.16 ***
Water - active	-1.3 ± 0.10 ***	-1.2 ± 0.14 ***	-1.99 ± 0.07 ***	0.82 ± 0.09 ***
Water - intensive	-1.66 ± 0.11 ***	-0.81 ± 0.15 ***	-2.84 ± 0.07 ***	0.14 ± 0.05 **
Flying - intensive	-0.05 ± 0.08	-0.003 ± 0.11	-4.15 ± 0.06 ***	-0.12 ± 0.06
Flying - flap-glide	-3.7 ± 0.26 ***	1.2 ± 0.45 **	-1.53 ± 0.27 ***	-0.92 ± 0.17 ***
Flying - non-flapping	-2.9 ± 0.18 ***	1.0 ± 0.31 ***	0.003 ± 0.35	-0.39 ± 0.19
GPS-derived behaviours				
Search	-0.43 ± 0.11 ***	-0.74 ± 0.16 ***	1.39 ± 0.12 ***	-0.09 ± 0.12
Transit	-0.74 ± 0.11 ***	0.25 ± 0.17	1.49 ± 0.10 ***	-0.36 ± 0.11 ***

Table 4. Model coefficients for zero-inflated beta generalized linear mixed model predicting the effect of sun angle on the probability of Bermuda petrels engaging in different behaviours during foraging trips (see Fig. 5).

depth (see references in [28, 51]), our TDR data suggest that the Bermuda petrel is a surface feeder with limited capacity to dive. According to the literature, seabirds' morphological and physiological characteristics should be good predictors of a species' specialization in flight behaviour over diving behaviours [26]. Along this continuum, the Bermuda petrel seems to be placed toward a consistent optimization of flight capacity at the expense of diving ability. As a corollary, this result adds additional evidence supporting the idea that the capture of meso-pelagic and bathypelagic prey must occur exclusively when these organisms are available in the very uppermost layer of the water surface. The accelerometer data from our study showed petrels spent approximately 80% of their time flying, with non-flapping flight being the most frequently used flight mode (on average 53%).

Foraging trip directions and petrel at sea distribution during incubation

Bermuda petrels foraged thousands of kilometers away from the breeding colony (average 1200 km) spending on average 10 days at-sea, similar to other *Pterodrom* species [14, 49, 50, 52]. They were consistent in their departing direction from the colony, as has been observed in the Murphy's petrels (*P. ultima*) [49], showing a clear preference for the NNE (Fig. 1), targeting the Gulf Stream [16, 31]. The pelagic area in which the "search" activity occurred (Fig. 1B) overlapped significantly with that identified by Campioni et al. [16] for birds tracked in previous years. However, in the present study, we recorded for the first time ever, a bird foraging off the continental shelf of North Carolina USA (see Fig. 1), which was the third major foraging area for *P. cahow* identified by Madeiros et al. [53] using geolocator tags.

Activity budget and daily activity pattern

When at sea, Bermuda petrels spent more than three quarters of their time in flight with non-flapping flight being the most common behaviour under all conditions. Our results are in line with the flight strategy expected by a dynamic soaring species. Such a flight strategy enables petrels and related species, including albatrosses and shearwaters, to travel for days without resting, limiting their energy expenditure [54, 55]. Although we did not include environmental variables in our analysis because most at-sea activity data came from biologgers without GPS sensors, previous works provides evidence for the selection of favourable wind directions to support the extremely long-ranging movements and foraging success of some petrel species [14, 16, 56].

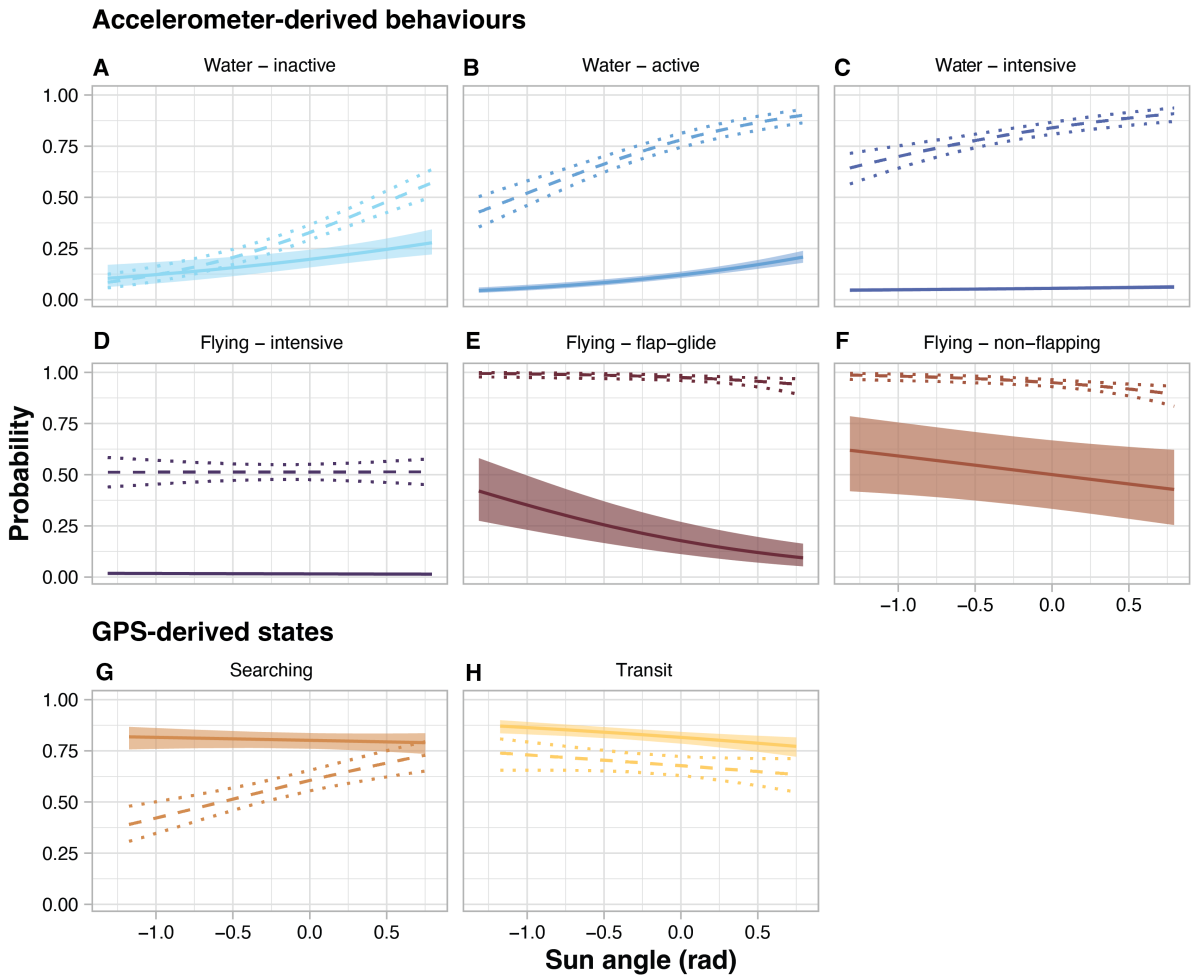

Figure 5. Predicted effect of sun angle on the time spent in different behaviours during trips by incubating Bermuda petrels. Models were run using behavioural modes derived from accelerometer (A-F) and GPS data (G-H). Dashed lines show the probability that each behaviour will occur and dotted lines are 95% confidence intervals. Solid lines show the proportion of time petrels were predicted to engage in each behaviour conditional on the probability that the behaviour occurs (shaded areas are 95% confidence intervals).

In general, petrels were more active and more likely to spend time on the water during the day (Fig. 5). All three water behaviours were more likely, in terms of both occurrence and proportion of time, at higher sun elevations (Fig. 5). The intensive water behaviour included bursts of "hyperactivity" which may suggest scavenging and seizing dead and/or live prey on the water surface. Scavenging is the most likely feeding mode to explain the occurrence of very large squids in petrels' stomach content [10, 11]. However, without external validation it is impossible to be certain that this water-intensive behaviour reflects a surface foraging activity.

How birds access prey or which group of prey are available, particularly by day, to specialized mesopelagic predators with limited diving ability as the Bermuda petrel, remains little understood. The ecology of their prey and the occurrence of oceanographic features may help to shed light on it. For instance, mesoscale oceanographic processes including eddies, can influence the seasonal presence of mesopelagic lanternfish larvae including their vertical distribution, with <20% of lanternfish larval density found between 0–20 m depth in winter, and >25% occurring in summer in the same layer ([**?**]). Bermuda petrel foraging activity is known to be associated with mesoscale eddies, which aggregate prey ([**?**]). Furthermore, at least two of the three squid species preyed by the Bermuda petrel [16] show a planktonic embryo stage before the young squids grow and take up a benthic existence as adults (*Stigmatoteuthis hoylei* and *Histioteuthis corona* in https://www.sealifebase.ca/search.php). Indeed, it is most

probable that it is during this stage of squids' life cycle when petrels are most likely to catch them.

Conversely to what we observed for water behaviours, the flight behaviours increased in occurrence and proportion of time with negative sun elevation values suggesting that, by night, petrels are particularly active "on the wings". It is plausible to believe, as suggested by our results (see Table 3) that all three flight behaviours could include the typical "aerial dipping" of *Pterodorma* petrels [19, 20], which will explain how and when birds can access deep sea prey performing the diel vertical migration.

By combining our results with published information on *Pterodroma* petrel activity pattern, it emerges that the degree of nocturnal activity in this group is quite flexible, thus only few of them are predominantly nocturnal [57]. Furthermore, nocturnality changes along the annual cycle, across breeding stages and is influenced by moon illumination [57, 58]. For instance, during incubation, the Chatham petrel, *P. axillaris* spent a lower proportion of time on water by day [58], while the Atlantic petrel, P. incerta and the *P. cahow* exhibit similar proportions by day and night [16, 59]. Unfortunately, due to the restricted tracking period, we were not able to test the effect of moon phase on petrels' activity pattern which, in turn may be also affected by the behavioural response of their prey to changes in moonlight levels [60].

Finally, it is worth noting that some discrepancies can emerge in the activity budgets when different technologies (e.g., geolocator, GPS, accelerometer) and analytical methods are employed to infer behaviours. Our study exemplified this issue. Here, the GPS-derived behaviours were less informative compared to the accelerometer-derived behaviours which instead, allowed to discriminate birds' activities at a finer scale (Fig. 5).

Conclusion

Overall, this study provides new insights into the foraging behaviour of an endangered gadfly petrel, having potential implications for evaluating the species' risk of interaction with at-sea anthropogenic activities. For instance, the crossing of vast portions of oceanic areas for foraging, and their nocturnal flight activity makes the species highly vulnerable to the presence and light-driven attraction to oil and gas infrastructures [31], shipping and commercial fishing vessels operating in the western North Atlantic. Particularly, our insights regarding petrels' surface feeding strategy and scavenging behaviour might help to develop target actions focused to reduce the risk of attraction to fishing boats for feeding on discarded bait or fish offal.

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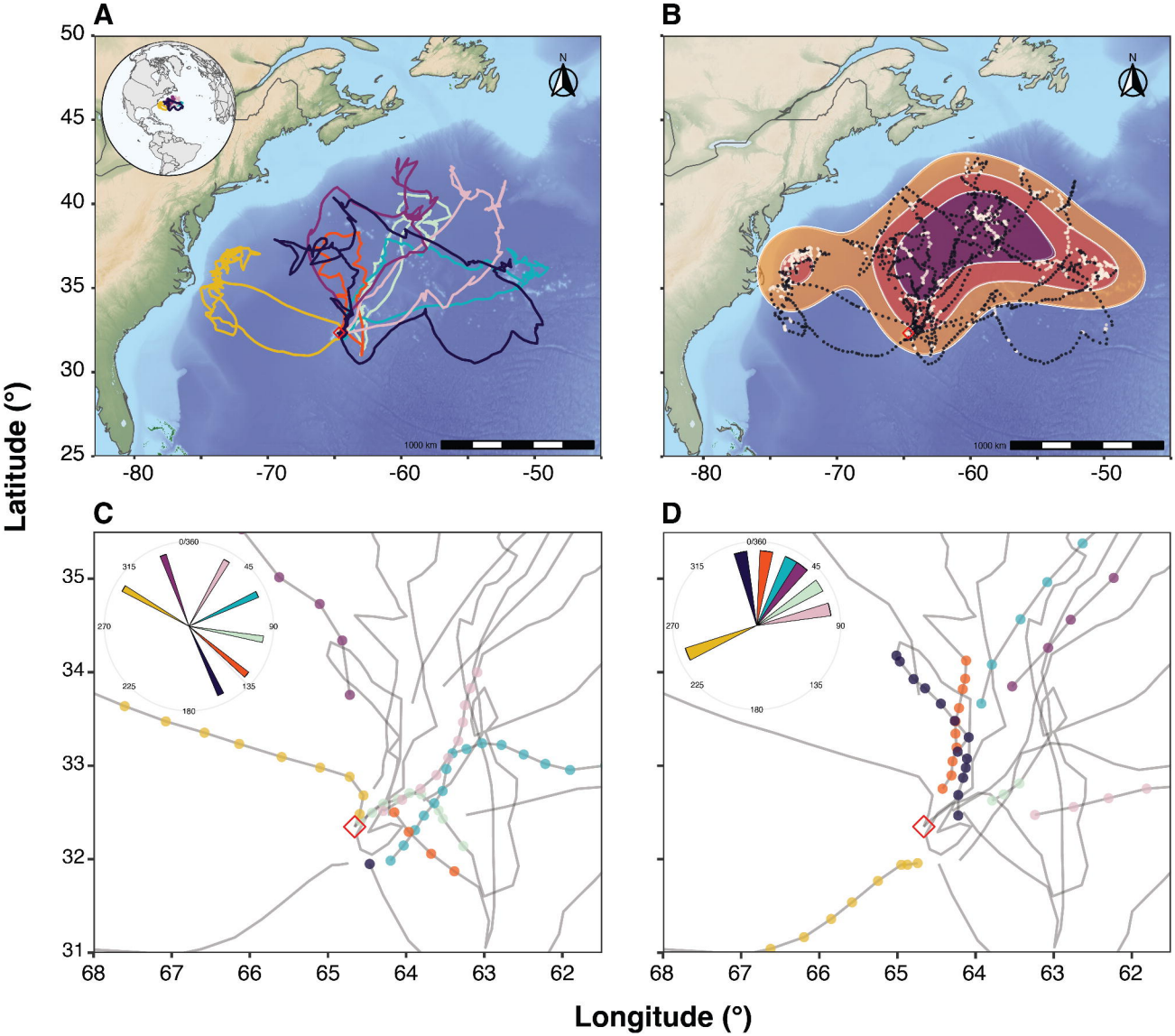
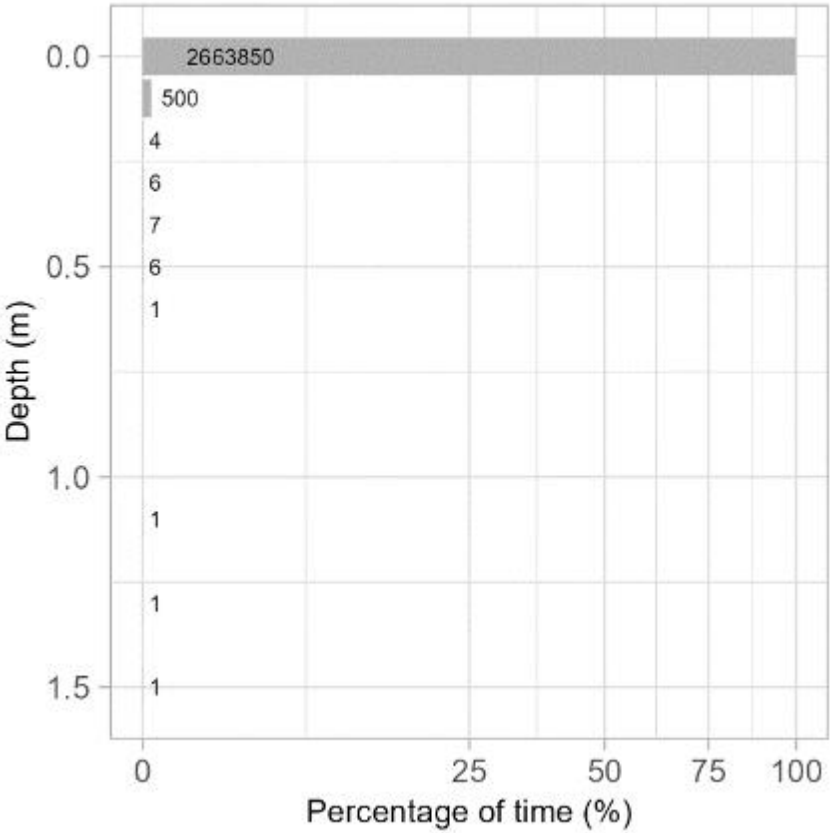
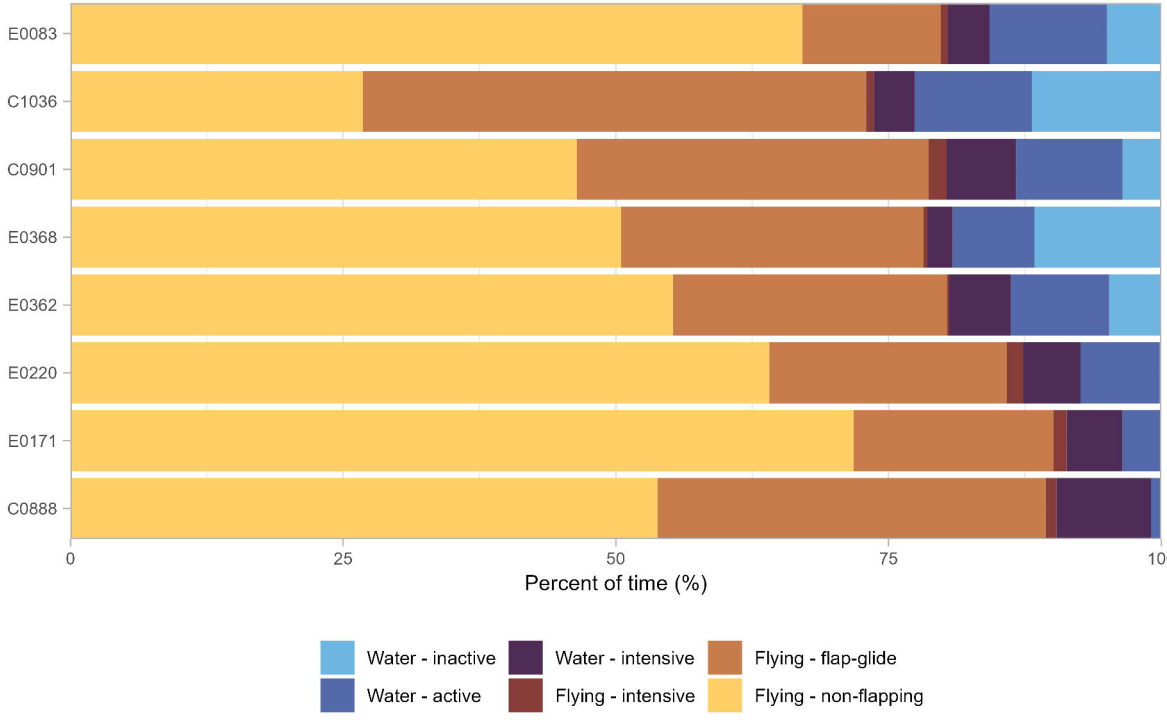
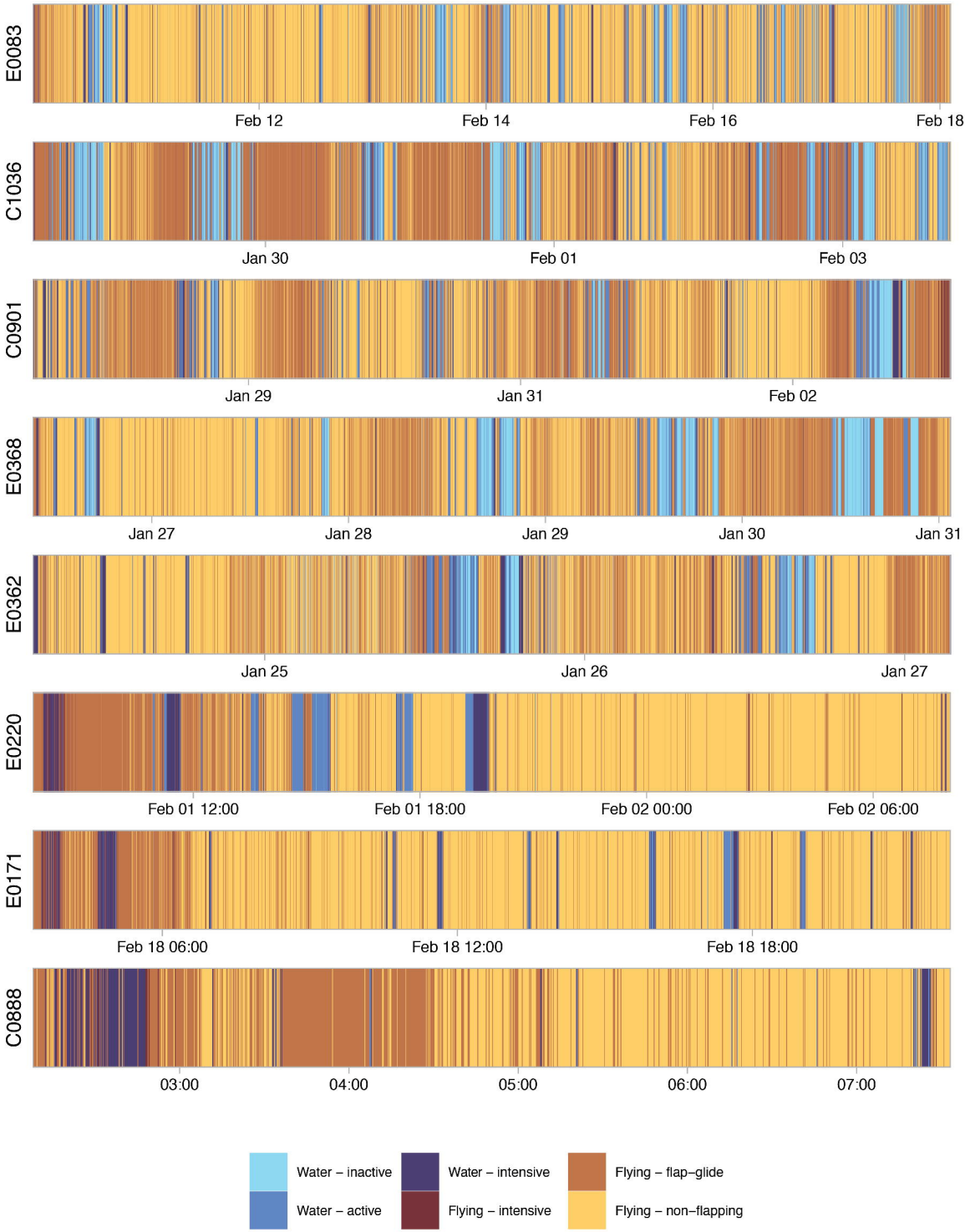
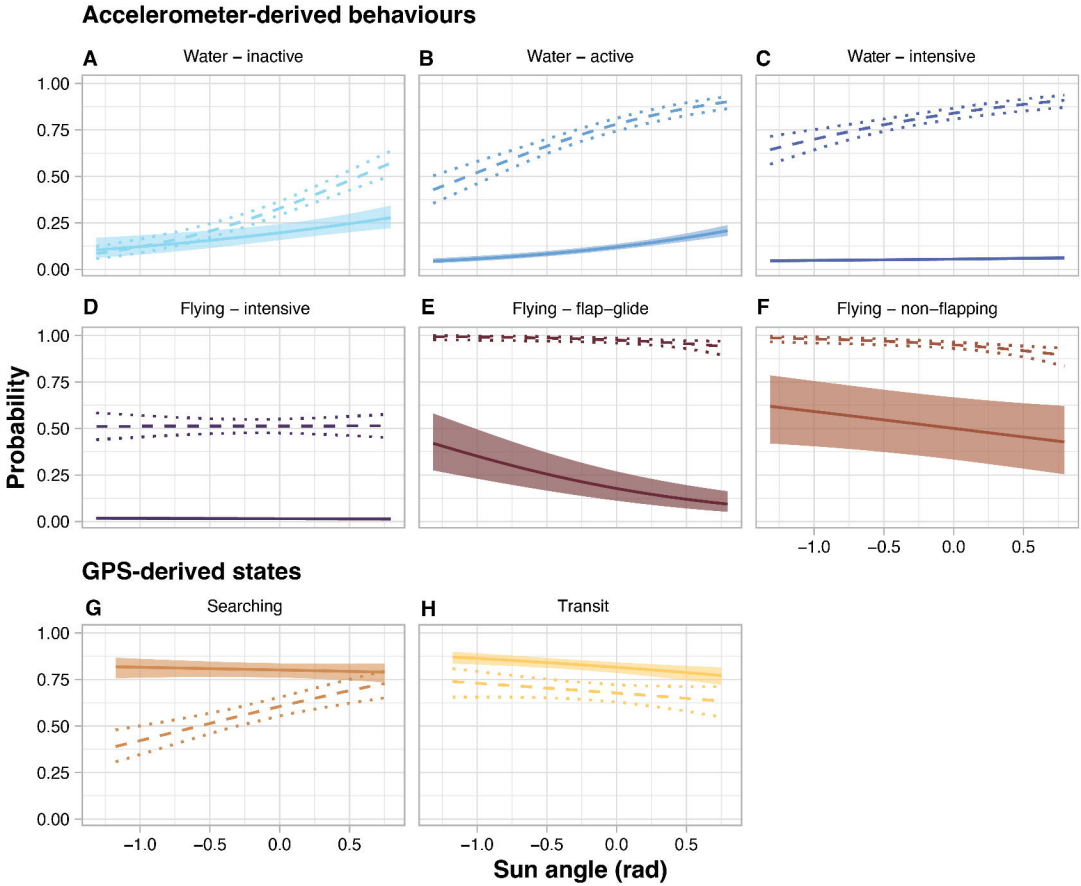

A
B
C
D
Latitude (°)
Longitude (°)
50
45
40
35
30
25
-80
-70
-60
-50
N
1000 km
35
34
33
32
31
68
67
66
65
64
63
62
0/360
45
90
135
180
225
270
315


0.0
0.5
1.0
1.5
Depth (m)
2663850
500
4
6
7
6
1
1
1
1
0
25
50
75
100
Percentage of time (%)


E0083
C1036
C0901
E0368
E0362
E0220
E0171
C0888
0
25
50
75
100
Percent of time (%)
Water - inactive
Water - active
Water - intensive
Flying - intensive
Flying - flap-glide
Flying - non-flapping


E0083
Feb 12
Feb 14
Feb 16
Feb 18
C1036
Jan 30
Feb 01
Feb 03
C0901
Jan 29
Jan 31
Feb 02
E0368
Jan 27
Jan 28
Jan 29
Jan 30
Jan 31
E0362
Jan 25
Jan 26
Jan 27
E0220
Feb 01 12:00
Feb 01 18:00
Feb 02 00:00
Feb 02 06:00
E0171
Feb 18 06:00
Feb 18 12:00
Feb 18 18:00
C0888
03:00
04:00
05:00
06:00
07:00
Water – inactive
Water – active
Water – intensive
Flying – intensive
Flying – flap–glide
Flying – non–flapping


Accelerometer-derived behaviours
A
Water – inactive
B
Water – active
C
Water – intensive
D
Flying – intensive
E
Flying – flap–glide
F
Flying – non–flapping
GPS-derived states
G
Searching
H
Transit
Probability
1.00
0.75
0.50
0.25
0.00
−1.0
−0.5
0.0
0.5
Sun angle (rad)