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RESEARCH ARTICLE

Flight style and time–activity budgets of the smallest petrels

Federico De Pascalis^{1,*}, David Grémillet^{2,3}, Andrea Benvenuti⁴, Francesco Ventura⁵, Valeria Jennings⁴, Diego Rubolini^{6,7} and Jacopo G. Cecere¹

ABSTRACT

Procellariiforms are the most oceanic among birds, regularly embarking on the longest journeys in the animal kingdom to find food over an apparently featureless sea surface. To minimize energy expenditure, many species harness wind energy through dynamic soaring, extracting kinetic energy from the wind shear. The smallest members of this order, storm petrels, have functional traits that prevent this type of locomotion, and are predicted to rely on flapping flight despite their high motility. However, theoretical predictions have never been validated and their flight strategy and activity budgets are unclear. We hypothesized that, as the benefits of dynamic soaring are out of reach, these birds should rely on gliding to some extent to sustain their long-ranging movements and save energy. To test our hypothesis we used, for the first time, miniaturized inertial measurement units on one of the world's smallest seabirds, the Mediterranean storm petrel (*Hydrobates pelagicus melitensis*). We demonstrate that these small seafarers spend 78% of the time flying during their foraging trips, with wingbeat frequencies up to 15 Hz. During transiting flight, they flap their wings at high frequency (mean±s.d.: 8.8±0.8 Hz) for 91% of the time, gliding sporadically and only for an instant (mean±s.d.: 0.11±0.17 s). Flight activity was high during the night and early morning, while they rested on the sea in the central hours of the day. Overall, our results reveal a peculiar locomotory strategy among procellariiforms and raise questions about how they can energetically sustain foraging trips spanning hundreds of kilometres.

KEY WORDS: Accelerometry, Magnetometry, *Hydrobates pelagicus melitensis*, Storm petrel, Gliding, Flapping

INTRODUCTION

Hypermobile procellariiform seabirds are adapted to an oceanic existence, being depicted as the ocean wanderers par excellence. During reproduction, they engage in foraging excursions that are the longest of the animal kingdom, roaming the oceans to find prey (Ventura et al., 2020). To sustain this seafaring lifestyle, many species are known to fly harvesting energy from the environment, thereby

reducing drastically – up to 90% – their energy costs, moving with little effort (Shepard, 2022). Indeed, in our imagination, these species are supremely adapted to operate in the ever-changing space that is the ocean–air interface, leveraging the kinetic energy that forms in this turbulent layer to their favour (Sachs et al., 2013). An archetypal case are albatrosses, the largest procellariiforms (2–9 kg; Tobias et al., 2022), which flap their wings for 1–5% of their time in flight only, dynamically soaring across wind gradients (Richardson, 2011; Sakamoto et al., 2013; Sato et al., 2009). Albatrosses have deep roots in human culture, often embodying the meeting between human beings and the marine realm (Mäenpää, 2020), and their flight mode has inspired technological innovation and engineering (Mathew et al., 2021). Many studies have now described in detail how they negotiate winds to successfully operate in the waters they inhabit (Schoombie et al., 2023; Weimerskirch et al., 2000). Stemming from this knowledge, later deepened via a vast amount of biologging studies on sister species, smaller procellariiforms have been shown to be capable of using dynamic soaring to different extents (Paiva et al., 2010; Sato et al., 2009; Spivey et al., 2014; Ventura et al., 2020). However, storm petrels, the smallest procellariiforms, occupy the opposite end of the body mass spectrum from albatrosses (16–90 g; Tobias et al., 2022), which prevents them from using dynamic soaring. Indeed, below a certain size threshold, flapping flight becomes more advantageous (Hedenstrom, 1993). This, combined with their wing morphology, suggests a flight mode characterized by rapid wingbeats (Pennycuik, 1996). The recent miniaturization of GPS trackers has unravelled the hypermobility of this group, describing a foraging range spanning hundreds of kilometres, covered every 2 days during incubation bouts (De Pascalis et al., 2021; Medrano et al., 2022). The image of a bird, the size of a swallow, navigating through waves and winds over vast areas, flapping their wings at high frequency trip after trip, is indeed evocative and raises questions about their energy-saving capabilities and time–activity budgets. Such questions can be answered only using high-resolution data, such as acceleration or orientation recordings. The latter, however, have until now been out of reach because of technological limitations, also preventing validation of theoretical predictions on their flight.

The overarching goal of this study was to describe, for the first time, the flight mode and at-sea time–activity budgets of storm petrels. To do so, we used custom-designed miniaturized inertial measurement units (IMUs: tri-axial accelerometers–magnetometers–temperature loggers). We hypothesized that birds should primarily adopt a flapping technique, in accordance with theoretical predictions, and that they should rely to some extent on passive flight (gliding) to energetically sustain their long-ranging movements.


MATERIALS AND METHODS

IMU deployment

In 2022, we tagged 12 incubating storm petrels, *Hydrobates pelagicus melitensis* (Schembri 1843), breeding in Sardinia, Italy (40°35'18" N, 8°10'24" E) with IMUs (Axy5, TechnoSmart, Colleverde, Italy). The units were firmly attached on the back

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feathers of birds, as close as possible to their centre of mass, using three thin strips of Tesa tape (mean±s.d. bird body mass: 32±2 g; device mass: 1.2±0.07 g with attachment; 3.8% of bird body mass, range 3.2–4.4%). IMUs were always attached in the same position, with the *x*-, *y*- and *z*-axes of the device aligned with the antero-posterior (surge), medio-lateral (sway) and dorso-ventral (heave) axes of the bird. Prior to deployment, the units were carefully calibrated. Specifically, magnetometers were calibrated following Gunner et al. (2021), while accelerometers were calibrated following Garde et al.'s (2022) 6-O method. As, to the best of our knowledge, there are no data available from accelerometers on storm petrels, and their fine-scale movement patterns were until now unknown, we tried a range of different settings (see [Supplementary Materials and Methods 1](#) and [Table S1](#)). Nine units were retrieved, after ca. 5 days (range 3–12 days), and only those with magnetometry data were retained for the analyses ($N=7$, see below). No evident detrimental effect of the units was noted (see [Supplementary Materials and Methods 2](#)). At device retrieval, we measured wing morphology, specifically folded wing length, wingspan, wing area, wing loading and aspect ratio ([Supplementary Materials and Methods 3](#)). Capture, handling and tagging procedures were carried out under the supervision of the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992 [Art.4(1) and Art 7(5)], which regulates research on wild bird species, and with permission of Parco Naturale Regionale di Porto Conte.

Data processing

Tri-axial accelerometer and magnetometer sensors were aligned with the NED coordinate system (i.e. *x*-North, *y*-East, *z*-Down). Magnetometer readings were corrected *post hoc*, to account for eventual hard and soft iron distortions that can interfere with the detection of the Earth's true magnetic field, using scale biases with orthogonal rescaling (Gunner et al., 2021). Accelerometer readings were corrected *post hoc* as well, to reduce sensor-induced errors, using a two-step procedure where both a correction factor and a gain are applied to each recorded value (Garde et al., 2022). We then derived a series of movement metrics from IMU data. Static acceleration was computed using a 1 s running mean and dynamic acceleration was computed by subtracting static acceleration from total acceleration. The vectorial sum of dynamic acceleration of the three axes was calculated to obtain the vectorial dynamic body acceleration (VeDBA), a proxy of energy expenditure (Wilson et al., 2020; but see Connors et al., 2024, for dynamic soarers). Pitch and roll, representing posture expressed in Euler angles (vertical and lateral body orientation, respectively) and heading (0–360°), computed via the tilt-compensated compass method (Gheorge, 2017), were calculated using the Gundog.compass function (Gunner et al., 2021). Their standard deviations (s.d., circular for heading) were calculated over a 5 s running mean, as well as the circular mean for heading. Wing beat frequency was obtained by extracting the dominant frequency in the *z*-axis using a fast Fourier transformation over a 1 s moving window, similar to Patterson et al. (2019).

Behavioural inference

Considering the lack of validation tools (such as bird-borne cameras or saltwater immersion sensors), we aimed to detect three coarse behavioural states: sitting on the sea surface, fluttering flight (probably associated with area-restricted search and feeding events) and sustained and directional flight (transiting). We visually inspected the variation in the movement metrics along the recording time series, and we selected three non-collinear ones

($r<0.3$; circular s.d. of heading, s.d. of roll and VeDBA) that were closely related to the target behaviours based on (1) our knowledge of the study species; (2) a careful evaluation of the frequency distributions of all variables (Collins et al., 2015) and (3) previous studies (Connors et al., 2021; Patterson et al., 2019). To identify behaviours, the three variables were summarized along 10 s fixed time windows and were used as input for a multivariate hidden Markov model (HMM) (Connors et al., 2021; McClintock and Michelot, 2018). The time window was arbitrarily selected as a compromise between noise reduction and avoiding masking behaviourally driven signals (Chimienti et al., 2022). As we were interested only in at-sea behaviours, each raw IMU data file was carefully inspected and foraging trips were visually selected in Framework4 software (<https://framework4.swan.ac.uk/>), given that the transitions between at-colony and flying (and vice versa) are easily identifiable using raw accelerometer data. We fitted a single three-states HMM to the whole dataset using the Viterbi algorithm to estimate the most likely behavioural state sequence (Zucchini et al., 2017) via the momentuHMM R package (McClintock and Michelot, 2018). Distributions for the variables used as data streams in the models were inspected, compared and selected using the fitdistrplus R package (Delignette-Muller and Dutang, 2015). We used a Gamma distribution for circular s.d. of heading, a normal distribution for VeDBA and a lognormal distribution for s.d. of roll (no zero-mass parameter was needed for the Gamma and the lognormal distributions). To ensure an appropriate selection of initial parameters, we ran a set of candidate models ($N=500$) iteratively using a range of randomly selected priors with reasonable values and compared the log-likelihood values. We modelled the transition probabilities of the HMM as a function of hour of the day following a 24 h cycle, using the cosinor function, to inspect (and account for) the circadian rhythm of individuals. Details on the fitted HMM, including the transition probability matrix and the pseudo-residuals can be found in [Supplementary Materials and Methods 4](#), [Table S2](#) and [Figs S1](#) and [S2](#).

Gliding and flapping flight

To quantify the reliance of storm petrels on flapping flight, we selected segments of transiting flights across the 10 foraging trips, and any point in transiting with VeDBA ≥ 0.3 g was labelled as flapping, while those with VeDBA < 0.3 g was labelled as gliding. This threshold was based upon previous studies (Garde et al., 2023; Collins et al., 2015), and upon the rationale that birds that are not moving have a similar value (see [Table 1](#)). Then we calculated the proportion of flapping flight used during transiting. Further, we calculated the duration of bouts of gliding and calculated a set of summary statistics (mean, median, standard deviation, maximum), removing cases in which gliding was identified only once in the time sequence, as it is not possible to calculate duration for one point in time only. Moreover, we removed 20 gliding bouts identified

Table 1. Data streams used to fit a hidden Markov model (HMM) for identifying behaviours from IMU data

Data stream	State 1	State 2	State 3
VeDBA (g)	0.77±0.07	0.21±0.08	0.81±0.21
s.d. of heading (rad)	0.26±0.21	0.36±0.27	0.46±0.29
s.d. of roll (deg)	2.35±1.41 (0.68, 0.61)	3.28±2.54 (0.89, 0.80)	6.42±5.50 (1.7, 0.51)

Estimates (means±s.d.; with location and scale in parentheses for s.d. of roll) of data stream distributions in the HMM. State 1 indicates transiting flight, state 2 rest and state 3 fluttering flight.

as outliers (0.002% of the data) whose duration (mean±s.d.: 227±368 s) exceeded the maximum glide duration (15 s) observed in the Manx shearwater (*Puffinus puffinus*), a procellariiform one order of magnitude larger than storm petrels (426 g; Spivey et al., 2014). It should be noted that given the nature of the data, we did not aim at identifying dynamic soaring cycles but passive gliding flight only.

RESULTS

Behavioural inference

We related the three HMM-identified states to distinct behaviours (Table 1; Supplementary Materials and Methods 4 and Fig. S1). State 1 was characterized by a relatively high and constant body acceleration, a strong movement directionality and a small variation in roll angle, indicating sustained transiting flight. State 2 was stationary, with a mixed variation in orientation and roll angle, indicating sitting on the sea surface. State 3 was characterized by strong and variable acceleration, sudden and extremely frequent changes of heading and a high variation in roll angle, indicating fluttering flight, a behaviour indicating an interaction with the environment, probably related to active food search and feeding events. The high variation in both VeDBA and s.d. of roll (Table 1) in this state reflects the peculiar foraging strategy of storm petrels. They can pick up small food items from the surface while flying, sometimes pattering on the sea surface, and often they land on the water for some seconds, holding their wings open and eating small floating organisms (Withers, 1979).

Flight style

During their foraging excursions, storm petrels spent overall a large amount of time (78%) on the wing (i.e. 42% transiting flight, 36% fluttering flight). The remaining 22% was spent resting on the sea surface, with minimal movements and low energy expenditure. These resting bouts were more likely to happen during the central hours of the day, while storm petrels were more active during the night-time (Fig. 1). During the transiting bouts, when storm petrels have a sustained and oriented flight, they flapped their wings for most of the time (91%) at a high frequency (mean±s.d.: 8.8±0.8 Hz; range 1.1–11.9 Hz, Fig. 2). The remaining 9% of the time comprised very

short gliding segments typically lasting less than 1 s (mean±s.d.: 0.11±0.17 s, median: 0.04 s, maximum value: 10.7 s). The highest wing beat frequency (15 Hz) was recorded during a fluttering flight segment (mean±s.d.: 7.3±2.7 Hz; range 0–15.2 Hz).

DISCUSSION

We show that, unlike other hypermobile procellariiform species, the flight strategy of small storm petrels was dominated by high-frequency wing flapping (8.8 Hz during transiting flight), aligning with theoretical predictions [9 Hz based on Pennycuick's (1996) model, applied using mean measurements from tracked birds; see Supplementary Materials and Methods 3]. During transiting flight, gliding segments were infrequent and of very short duration, and overall birds spent most of their time at sea on the wing. This flight strategy is similar to that of passerines, which, in contrast, spend significantly less time flying during foraging trips (13.3% versus 78%; Yu et al., 2024) and have foraging ranges several orders of magnitude smaller. Indeed, passerines embark on long-distance movements only twice per year during migration, while storm petrels routinely cover similar distances to forage throughout the whole breeding season (De Pascalis et al., 2021). Locomotion based on flapping flight has the advantage of allowing flexibility against wind conditions, favouring fast movement along more direct routes (Thorne et al., 2023) and counteracting displacement in strong winds (Hedenstrom, 1993), two key advantages for such small-bodied birds. However, this motion entails major energetic costs as wing beat frequency is strictly related to flight cost and power (Usherwood et al., 2011; but see Krishnan et al., 2022). For this reason, flapping flight has been identified as the most energetically expensive movement mode among vertebrates (Butler, 2016; Taylor et al., 2019).

In wing-flapping animals, crosswind should not reduce flight costs (O'Mara et al., 2019). The high selectivity of storm petrels for crosswinds (F.D.P., unpublished data) may suggest that other energy-harvesting mechanisms from the environment, while still relying on flapping flight, should be present to maintain a positive energy balance and counteract such energy costs. For instance, birds may derive additional energy by flapping their wings in rising air, such as vertical gusts near the waves (Alerstam et al., 1993;

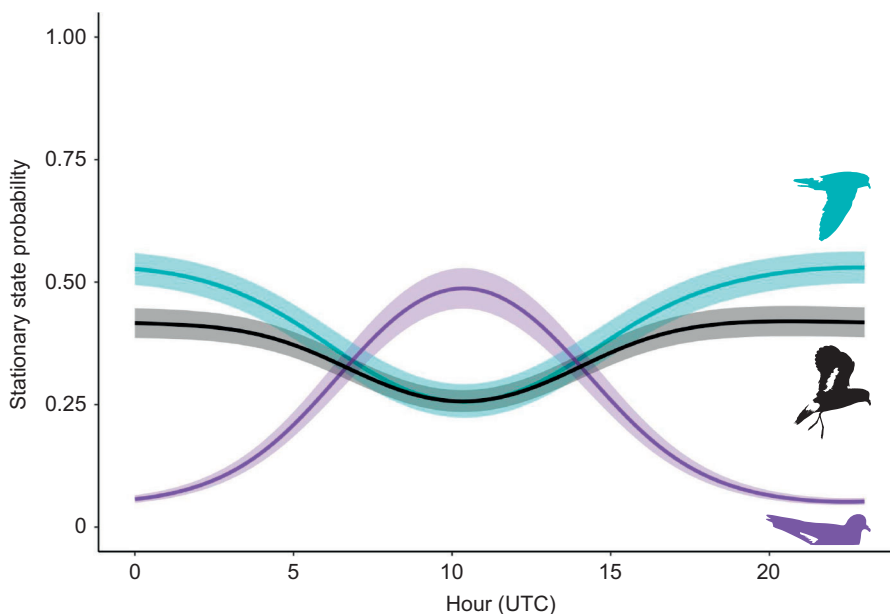


Fig. 1. Time–activity budgets of Mediterranean storm petrels. Time (hour-of-the-day)-dependent stationary state probabilities for three movement behaviours from the fitted hidden Markov model (HMM), representing time–activity budgets of incubating storm petrels [$N=7$; transit (blue), flutter (black), on water (purple)]. Solid lines indicate means and shaded areas are 95% confidence intervals.

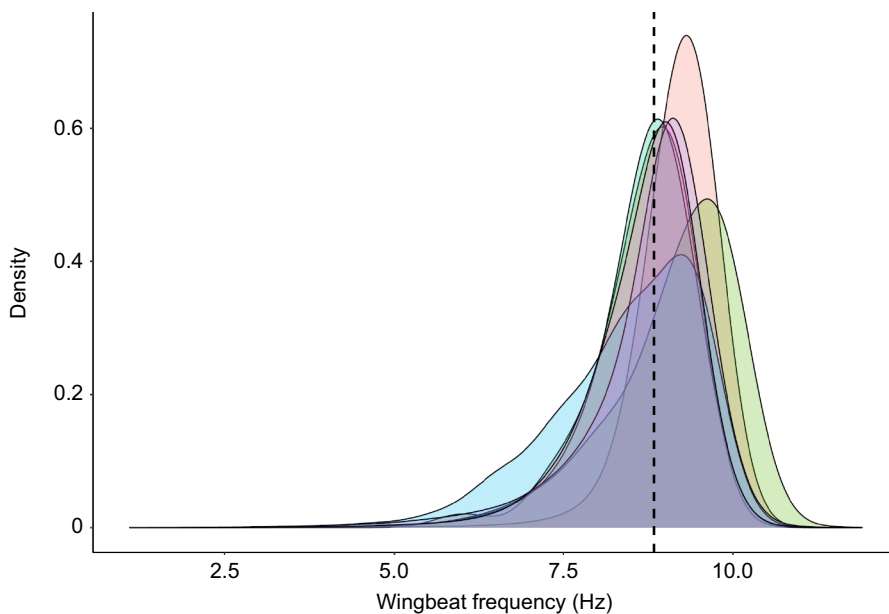


Fig. 2. Wing beat frequency of Mediterranean storm petrels. Kernel density plot of wing beat frequency of storm petrels during the transit phase. Each individual ($N=7$) is shown in a different colour, while the dashed vertical line indicates the cumulative mean.

Pennycuik, 2002) or in thermal updrafts (Garde et al., 2023), and close to the sea surface leveraging the ground effect (Norevik et al., 2023). This could lead to a search for local vertical updrafts, which may provide extra lift and help sustain gliding bouts. Those, albeit infrequent and extremely short in duration, allow storm petrels to save energy along 9% of their routes, highlighting that even short gliding bouts can be used as an energy-saving mechanism. Additionally, the high proportion of time spent fluttering suggests that the storm petrels fed frequently. Potentially, a high foraging frequency may be an important element to partially counteract the energy expenditure from prolonged flapping. Another implication of their flight mode is that the intense muscular contractions needed to sustain flapping flight for extended time generates metabolic heat, which strongly constrains flight speed and efficiency, ultimately limiting locomotory performance (Dyer et al., 2023). In this context, by resting on the water around midday (Fig. 1), storm petrels may aim to reduce the risk of critical hyperthermia resulting from excess body heat generated during flapping under the intense Mediterranean summer heat (Grémillet et al., 2012), a mechanism similar to that observed to be driving stop-and-go migration (Guillemette et al., 2016).

It should be noted that a flight strategy such as the one we described could be a prerogative of the smallest storm petrel species as larger species can use gliding more or to a longer extent (Camphuysen, 2007), or even of specific populations adapted to live in areas with light wind regimes. Moreover, it is also possible that birds rely more on flapping flight only as central place constraints increase (Thorne et al., 2023), given the need for a swift return to chicks. Ultimately, the energetic benefits of dynamic soaring are beyond the reach of storm petrels, and when at sea, they wing-flap over vast areas, possibly benefitting from the strategic energetic gains provided by flapping in updrafts and moving air. How storm petrels can afford such an expensive lifestyle whilst feeding on scattered, microscopic plankton items remains a mystery.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: F.D.P.; Data curation: F.D.P.; Formal analysis: F.D.P., V.J.; Funding acquisition: A.B., J.G.C.; Investigation: F.D.P., A.B., F.V., V.J., J.G.C.; Methodology: F.D.P., D.G., A.B., F.V., V.J., D.R., J.G.C.; Resources: A.B., V.J.; Supervision: D.G., D.R., J.G.C.; Writing – original draft: F.D.P., D.G., F.V., D.R., J.G.C.

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Data availability

Data used for this study at the 10 s time scale are available from <https://doi.org/10.6084/m9.figshare.27968322.v1>

ECR Spotlight

This article has an associated ECR Spotlight interview with Federico De Pascalis.

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