



Thermal soaring in tropicbirds suggests that diverse seabirds may use this strategy to reduce flight costs

Baptiste Garde¹, Adam Fell², Krishnamoorthy Krishnan¹, Carl G. Jones^{3,4}, Richard Gunner⁵, Vikash Tatayah⁴, Nik C. Cole^{3,4}, Emmanouil Lempidakis¹, Emily L. C. Shepard^{1,*}

¹Department of Biological Sciences, Swansea University, Swansea SA2 8PP, UK

²School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK

³Durrell Wildlife Conservation Trust, La Profonde Rue, Jersey JE3 5BP, UK

⁴Mauritian Wildlife Foundation, Grannum Road, Vacoas 73418, Mauritius

⁵Max Planck Institute of Animal Behavior, 78315 Radolfzell / Konstanz, Germany

ABSTRACT: Thermal soaring can offer substantial reductions in flight cost, but it is often assumed to be confined to a relatively narrow group of fliers (those with low wing loading relative to their body mass). Using high-frequency movement data, including magnetometry and GPS, we identified thermal soaring in a seabird previously thought to use only flapping flight: the red-tailed tropicbird *Phaethon rubricauda*. We tracked 55 individuals breeding on Round Island, Mauritius, and examined the environmental conditions that predicted thermal soaring in 76 trips (ranging from 0.8 to 43 h, mean = 5.9 h). Tropicbirds used thermal soaring and gliding flight for 13% of their flight time on average (range 0–34%), in association with both commuting and prey-searching/pursuits. The use of thermal soaring showed strong variation between trips, but birds were more likely to soar when flying with tailwinds. This enables them to reduce their flight costs without a substantial increase in trip duration, which is pertinent in the breeding season when they are constrained by time and the need to return to a central place. Birds may therefore be able to increase the amount of thermal soaring outside the breeding season. Overall, we suggest that thermal soaring may be more widespread than previously thought, given that birds without specific morphological adaptations for this behaviour can soar for extended periods, and the bio-logging approaches best-placed to detect thermal soaring (high-frequency GPS/magnetometry) tend to be used during the breeding season, when thermal soaring may be less likely.

KEY WORDS: *Phaethon rubricauda* · Flight · Energetics · Accelerometry · Biologging · Biotelemetry · GPS

1. INTRODUCTION

Diverse species of birds from 55 g bee-eaters *Merops apiaster* to 11 kg Andean condors *Vultur gryphus* use thermal updrafts to reduce their flight costs (Sapir et al. 2010, Williams et al. 2020), with some species gaining hundreds, even thousands, of metres

of altitude in thermals and using this altitude to glide over long distances (Weimerskirch et al. 2016). This low-cost form of transport is particularly advantageous when considered in relation to the costs of flapping flight, which become proportionately more costly with increasing body mass (Pennycuik 2008). Nonetheless, it is generally assumed that the species

*Corresponding author: e.l.c.shepard@swansea.ac.uk

that spend time circling and gaining altitude within thermal updrafts possess morphological adaptations for this type of flight. Wing loading (the mass divided by the wing area) is a good indicator of thermal soaring capacity because it predicts the sink rates, flight speeds and turn radii during gliding flight (Pennycuik 2008). Birds with low wing loading are able to fly more slowly and turn more tightly, enabling them to circle and climb within thermal updrafts, even when these are relatively weak and narrow, such as those that form over the ocean (Weimerskirch et al. 2016, Duriez et al. 2018).

The use of thermal soaring in terrestrial birds is generally determined by the availability of thermal updrafts (hereafter referred to as thermals) (Shamoun-Baranes et al. 2016). Thermals form when the surface heats the air above it, with air rising when it is warmer, and hence less dense, than the surrounding air. On land, there is a strong diurnal change in thermal availability and strength, both of which tend to peak around midday. This explains temporal patterns in the use of soaring flight over land (Shamoun-Baranes et al. 2016) as well as the flight height of soaring birds (Shamoun-Baranes et al. 2006). Thermal availability also varies in space, as thermals develop over parts of the surface that heat more rapidly or retain heat to a greater degree, including slopes orientated towards the sun and dark surfaces (Bradbury 1989, Sage et al. 2022). Surface characteristics predict the use of soaring flight in vultures and gulls at regional scales (Mandel et al. 2011, Scacco et al. 2019, Sage et al. 2022). Spatio-temporal changes in uplift potential also influence when and where terrestrial birds make sea-crossings (Becciu et al. 2020, Nourani et al. 2020, 2021).

Thermal activity is much weaker over water than over land; nonetheless, thermals over the water still represent an important source of energy for soaring birds, including gulls and migrating raptors (Woodcock 1975, Shamoun-Baranes et al. 2016, Duriez et al. 2018, Nourani et al. 2020). Indeed, frigate birds use thermal soaring for up to 82% of their migration (Weimerskirch et al. 2016). Frigate birds are thought to have the lowest wing loading among seabirds relative to their body mass (Spear & Ainley 1997) and the opportunities for low-cost flight, associated with thermal soaring, are thought to underpin their migration routes (Weimerskirch et al. 2016). The use of thermal soaring in other seabirds remains little studied (Duriez et al. 2018, Sage 2022). Nonetheless, thermals should be widely available in the trade wind zone where wind from higher latitudes moves over warm waters. Thermals should also be

fairly evenly distributed in this region, as the sea surface structure and temperature are relatively homogeneous compared to the mosaic of terrestrial substrates (which produces notable variation in land-surface temperature). Indeed, the recent, unexpected discovery of thermal soaring in red-tailed tropicbirds *Phaethon rubricauda* (Gunner et al. 2021a) demonstrates that even seabirds considered to be obligate flapping fliers use thermal soaring to reduce their costs of transport.

One factor that is likely to be critical in determining the profitability of thermal soaring over the ocean is the wind direction. In wind-still conditions, birds make no progress towards their destination as they circle within thermal updrafts. However, it is rarely wind-still in oceanic environments. Even weak winds create vertical shear that 'tilts' thermal updrafts (Weinzierl et al. 2016, Vansteelant et al. 2017). In order to remain within a thermal, birds must therefore move horizontally as well as vertically (Harel et al. 2016), leading to a downwind drift of the flight path. The energy savings that birds can accrue from thermal soaring in relation to distance will therefore depend on whether they are drifted towards or away from their direction of travel. This phenomenon is particularly pertinent when thermals are weak and birds must soar for longer for a given gain in altitude (Pennycuik 2008). The profitability of thermal soaring should therefore depend on thermal strength, wind strength and the difference between the wind direction and the bird's direction of travel (which can be expressed as the head- or tailwind component).

To understand how the physical environment affects flight costs, we need to quantify how weather, including wind, affects the profitability and use of thermal soaring. This is particularly important in the context of global changes in wind speed, air and sea surface temperature (Solomon et al. 2007, Young et al. 2011). In this study, we used GPS units and high-frequency, multi-sensor tags, equipped with magnetometers, accelerometers and barometric pressure sensors, to investigate thermal soaring in red-tailed tropicbirds. Tropicbirds breed throughout the year on Round Island, Mauritius, offering an opportunity to record their flight behaviour in seasonally changing conditions. Our specific objectives were to (1) assess the environmental and behavioural contexts in which tropicbirds use thermal soaring flight, (2) examine the relative profitability of soaring flight, in terms of the groundspeeds achieved and the use of flapping flight during thermal soaring, and finally (3) assess what this can tell us about the likely use of thermal soaring in other taxa, using aeronautical

models to compare the glide performance of tropicbirds with other seabird morphologies.

2. MATERIALS AND METHODS

Fieldwork was conducted with red-tailed tropicbirds nesting on Round Island, Mauritius (19.8486° S, 57.7885° E) (Gardner et al. 1985) during chick rearing in February, March, September and October 2018. Birds were weighed and photographed, following Pennycuik (2008), and these values were used to estimate wing loading, dividing body mass by wing area (the latter was calculated using the software ImageJ: <https://imagej.net/ij/index.html>). Tropicbirds were equipped with a Daily Diary (Wildbyte Technologies) and a GPS logger (GiPSy 5, Technosmart Europe). The Daily Diary recorded acceleration and magnetic field strength in 3 axes at 40 and 13 Hz, respectively, and barometric pressure and temperature at 4 Hz. The GPS was set to log 1 location per minute. Both loggers were placed in a zip-lock bag and fixed to the back feathers using Tesa tape. The loggers (including battery), housing and tape weighed 27.7 g, representing <3% of the average body mass (mean body mass for tagged birds was 826 g, range: 650–920 g; Table S1), and 4.3% of the lowest body mass recorded during this study (650 g). We excluded the short flights that were often observed immediately after tag deployment (and were therefore not associated with foraging), and incomplete trips (a consequence of tag failure). This produced a total of 76 flights recorded from 55 birds (Garde et al. 2022). Ethical permissions for the deployment of loggers on tropicbirds were granted by Swansea University Animal Welfare and Ethical Review Body (permit 040118/39).

Flight altitude above sea level was calculated from the barometric pressure recorded by the Daily Diary, adjusted for daily changes in mean sea-level pressure, downloaded from <https://earth.nullschool.net/> with a resolution of 3 h and $0.5^\circ \times 0.5^\circ$. Raw pressure values were smoothed over 2 s, and the rate of change in altitude (V_z) was calculated over 1 s intervals. Groundspeeds (V_g) were taken as the haversine distance between GPS fixes divided by the time difference.

A portable weather station (Kestrel 5500L, Kestrel Instruments) mounted on a 5 m pole at the highest point of Round Island (latitude: 19.850400° S, longitude: 57.788837° E, 265 m ASL) recorded temperature, relative humidity, wind speed and direction every 5 min.

We used the difference in air and sea temperature (ΔT) as a proxy for thermal uplift potential (Duriez et al. 2018, Nourani et al. 2020, 2021, Sage et al. 2022). Here, higher positive values of ΔT indicate that sea surface temperature was greater than the air temperature, with stronger uplift potential (Woodcock 1975, Duriez et al. 2018). We took air temperature records from the weather station after confirming that temperature measurements made by the station were strongly correlated with estimates from ERA5 (Pearson correlation test: $t = 248.95$, $df = 14559$, $p < 0.0001$, correlation coefficient = 0.9). Sea surface temperatures were obtained from <https://earth.nullschool.net/>, combining the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA, <https://ghrsstpp.metoffice.gov.uk/ostia-website/index.html>) and Real Time Global Sea Surface Temperature (RTGSST, <https://polar.ncep.noaa.gov/>) satellite-based observation products (with temporal resolution of 3 h and spatial resolution of $0.5^\circ \times 0.5^\circ$).

We used wind values from the weather station in our analyses as they provided high resolution information on changes in wind speed associated with weather fronts, compared to ERA5 estimates of wind speed, which are available with hourly resolution ($0.25^\circ \times 0.25^\circ$ spatial resolution). Measurements by the weather station on Round Island were interrupted due to battery failure between 9 and 20 February, during which 7 flights were recorded. These values were replaced by hourly wind records from Sir Seewoosagar Ramgoolam International Airport in Mauritius (latitude: 20.433640° S, longitude: 57.678618° E), approximately 65 km from Round Island (www.wunderground.com). We examined whether our results were affected by the inclusion of these data by running models with and without tracks on 9 and 20 February. Excluding these flights did not change the modelled results.

2.1. Classification of flight types

Flight was readily identifiable from the barometric pressure data recorded by the bird-borne loggers, as this varied continuously during flight due to changes in flight height. Flight data were further classified as flapping and non-flapping (hereafter termed ‘passive’ flight) using acceleration data (see next paragraph). Passive flight was then classed as either gliding or soaring, where soaring was taken as periods of non-flapping flight when birds were extracting energy from the atmosphere, evident through increases in altitude, and gliding was taken as period

of non-flapping flight where birds were losing altitude (see next paragraph).

Flapping and non-flapping flight were distinguished using acceleration data as follows. The vectorial sum of the dynamic body acceleration (VeDBA) was calculated according to Wilson et al. (2020), using smoothed raw acceleration values over 2 s to derive the static component. VeDBA values were smoothed again over 2 s, to produce a metric that varied between high and low levels of activity. Any point in flight with $\text{VeDBA} \geq 0.3 g$ was labelled as flapping, and any point with $\text{VeDBA} < 0.3 g$ and a negative rate of change in altitude was labelled as gliding. Level flapping flight was taken as sections of flapping flight where the absolute rate of change in altitude was $< 0.1 \text{ m s}^{-1}$.

Periods of non-flapping flight were clearly associated with thermal soaring, which is characterised by periods of circling, evident in the magnetometer signal (Fig. 1), followed by descending flight. Slope soaring and dynamic soaring produce different signatures in the magnetometry data, which we did not observe in the tropicbird data (Shepard et al. 2011).

We defined thermal soaring as periods where birds were circling and gaining altitude. Circling was identified using one of the horizontal channels of the

magnetometer, where circling is evident as sine-waves with a maximum when the sensor faces magnetic north and a minimum when it faces south (Shepard et al. 2011). Each turn is therefore represented by a positive and a negative turning point, which were identified automatically using the custom-written animal movement analysis software DDMT (Wildbyte Technologies, <http://wildbytetechologies.com/software.html>). As the time taken to complete 1 circle was between 10 and 20 s, we labelled 5 s on either side of each turn point (1/4 of a circle) (Wilson et al. 2018) and excluded periods with fewer than 2 turns. The labelling of the different flight modes was done in R Studio (version 4.0.0) (R Core Team 2020).

Red-tailed tropicbirds are surface feeders known to target flying fish (Le Corre et al. 2003). We were interested to see whether thermal soaring was associated with prey pursuits. These pursuits were evident as rapid reductions in altitude combined with a brief switch to gliding flight and low-frequency changes in the acceleration data that indicate manoeuvring (Fig. 2). Due to the variability in the rate of change in altitude associated with prey pursuits, these events were identified manually using DDMT.

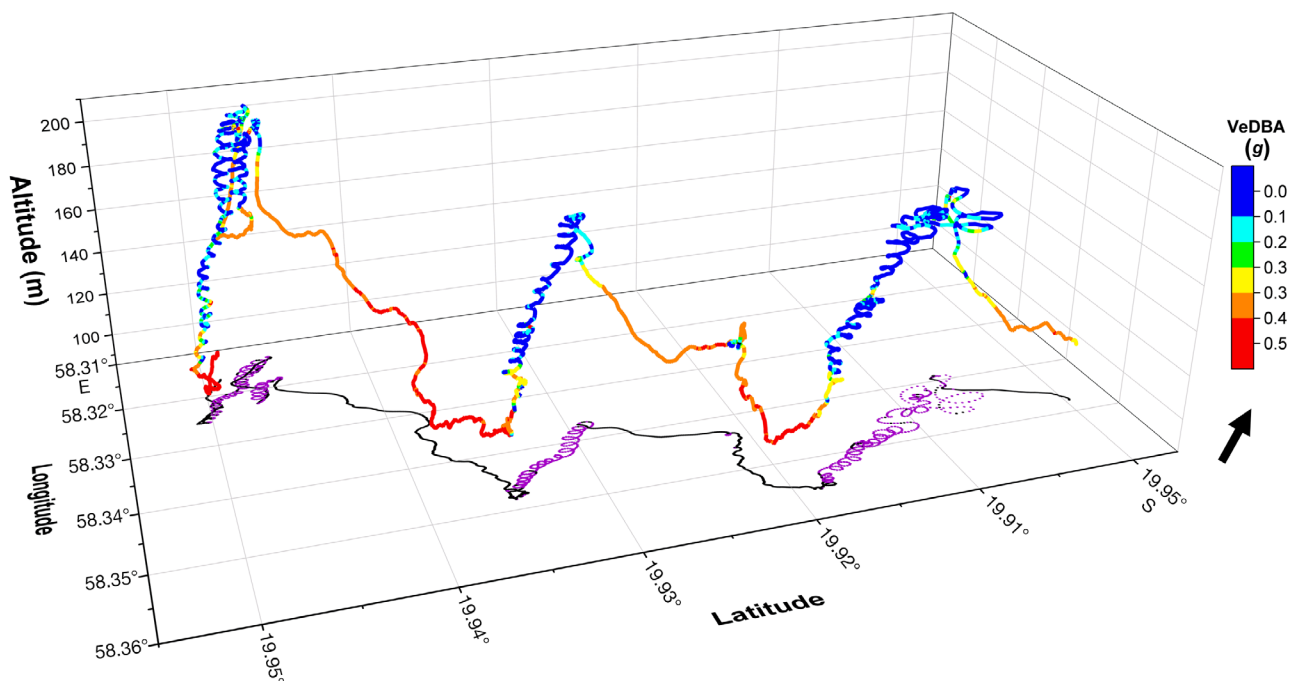


Fig. 1. A 45 min section of a tropicbird flight with periods of thermal soaring (with the bird flying left to right), modified from Gunner et al. (2021a). The track was reconstructed using the magnetometer data to derive the heading between consecutive GPS fixes, taking speed from the GPS (Gunner et al. 2021a,b). The dead-reckoned track is coloured according to a metric of activity, the vectorial dynamic body acceleration (VeDBA), where blue sections indicate periods without flapping. The 2 periods of descending flight with substantial flapping preceded likely prey pursuits. Flapping and soaring events are highlighted with black and purple in the x-y projection of the track. The black arrow indicates the wind direction (approximately 290°)

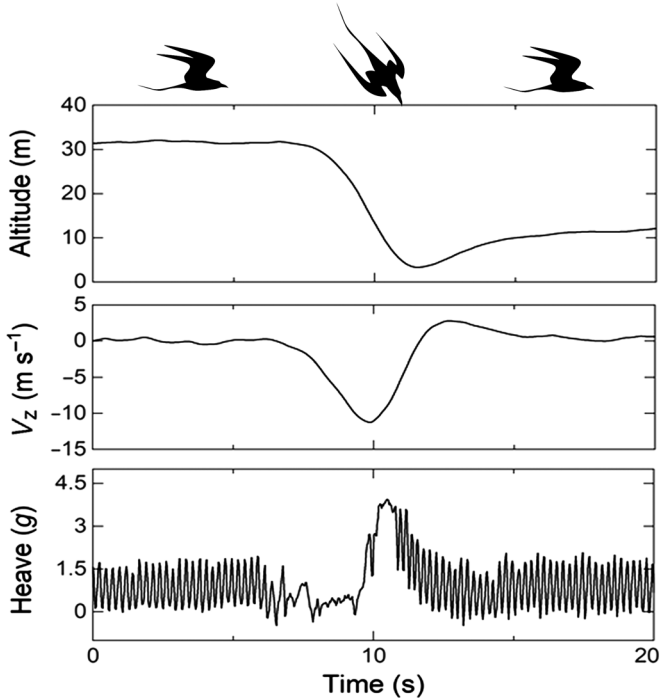


Fig. 2. Identification of aerial pursuits. Pursuits were typified by a loss of altitude (top panel), rapid vertical velocity (V_z), with negative values indicating descending flight (middle panel) and a switch from flapping to passive flight (any flight without wingbeats), as evident in the heave (dorso-ventral) acceleration values (bottom panel)

2.2. Statistical analysis

Seasonal differences in wind speed and ΔT were tested using Wilcoxon tests. We used a binomial generalised linear mixed effect model (GLMM) to model the likelihood that tropicbirds used passive flight. Specifically, we examined the effect of body mass, ΔT and tailwind component (TWC) on the presence/absence of passive flight, scoring the presence of soaring/gliding between successive GPS fixes as a binary variable with 0 corresponding to absence and 1 to presence (1 min GPS fixes, $n = 12\,675$). The TWC was calculated as the projection of the wind vector on the airspeed vector (Safi et al. 2013), estimated between successive GPS fixes. Positive values indicated a tailwind and negative values a headwind. Trip ID was included as a random factor to account for individual differences and route choice.

Inspection of the data revealed that tropicbirds flapped whilst circling within thermals as well as descending between them. We therefore also categorised bouts of circling flight according to whether they included flapping, and used a binomial GLMM to see if this was predicted by the TWC or ΔT ($n = 309$ bouts). We included body mass (numeric fixed effect)

and trip ID (random effect factor) in the model to account for individual and between-trip variation. Finally, we compared the climb rates of circling bouts (the total altitude gained during a circling bout divided by its duration) with and without flapping using a Wilcoxon test.

To understand the consequences of soaring and tailwind on the groundspeed, we classified segments between successive GPS fixes as level flapping flight or soaring/gliding. Segments were classed as soaring/gliding where at least 80% of flight was passive. Combining soaring and gliding was necessary due to the low number of segments with a complete absence of flapping. We used a GLMM (with Gaussian errors) that included body mass, flight mode, TWC and their interaction. To deal with temporal autocorrelation, we thinned the data set to select every second data point ($n = 1298$) and included the Ornstein-Uhlenbeck covariance structure (Gajda & Wyłomańska 2015) in the model, as residuals were still autocorrelated. Thinning of the data did not substantially change the sign of the estimated coefficients nor their size. Trip ID was used as a random effect to account for uncontrolled differences between trips.

Data analysis was conducted in R Studio using the R programming language (version 4.2.1) (R Core Team 2020). Mixed-effect models were built using the package ‘glmmTMB’ (version 1.1.4) (Brooks et al. 2017), with all attributes scaled to allow for the comparison between estimated coefficients, R^2 values were computed using the package ‘MuMIn’ (version 1.47.1) (Barton 2015), and models were tested for uniformity, overdispersion, significant outliers and temporal autocorrelation using the ‘DHARMA’ package (version 0.4.6) (Hartig 2017). While the model predicting groundspeed had a satisfactory QQ plot, it failed the test of uniformity; however, the 1-sample Kolmogorov-Smirnov test performed by DHARMA is highly sensitive to large sample sizes ($n = 1298$), which might have led to a lower p-value (Uhm & Yi 2021).

2.3. Use of soaring across species

We used aeronautical models to examine the gliding performance of tropicbirds and compared this to other seabird species. We calculated the wing loading of a tropicbird with an average mass from our study sample. We then compared this to other seabirds for which wing loading data were available for tropical or temperate species (we did not consider

species from the Southern Ocean, where strong winds prevent thermal development). Morphological data were taken from the 'Wings' database within the freeware 'Flight' (version 1.24) (Pennycuick 2008) or the review by Hertel & Ballance (1999). Wing loading values were examined in relation to the allometric prediction that wing area \propto mass^{2/3}, where the proportionality is approximated using the same relationship derived across 220 species as provided by Pennycuick (2008). Examining values in relation to this line allowed us to establish whether the wing loading for a given species was higher or lower than would be expected based on its mass alone.

The minimum sink rate for birds in gliding flight corresponds to the thermal velocity required for a bird to maintain altitude in rising air and could therefore be compared with our estimates of thermal velocity, gained by subtracting the estimated tropicbird sink rate from the overall climb rates recorded. We examined the minimum sink rates (an indication of the capacity to use thermal soaring) in relation to the energetic motivation to switch to soaring flight, by estimating the costs of flapping flight as multiples of basal metabolic rate. Seabirds with a low sink rate but a high cost of flapping flight should therefore have the ability and motivation to use thermal soaring. The costs of flapping flight were estimated using the R package 'afpt' (version 1.1.0.3) (Klein Heerenbrink et al. 2015) for each species where morphometrics were known ($n = 17$). Sink rates were estimated using the software 'Flight' (version 1.0 2010) (Pennycuick 2008). These packages use aeronautical theory to predict flight performance characteristics from basic morphological measurements such as body mass, wingspan and wing area (Klein Heerenbrink et al. 2015).

3. RESULTS

3.1. Predicting the use of soaring in tropicbirds

Wind conditions were fairly consistent between the 2 study seasons, with prevailing south-easterly winds that were slightly stronger in the summer (Wilcoxon test: $W = 502$, $p = 0.039$, mean summer and winter speeds of 5.0 and 6.3 m s⁻¹, respectively). There was a seasonal difference in air temperature (Wilcoxon test: $W = 1395$, $p < 0.0001$), with higher temperatures during the austral summer (February–March, mean = 24.9°C) than the winter (September–October, mean = 20.6°C). Sea surface temperature followed the same trend (28.9°C in February, 28.3°C in March,

24.0°C in September, 24.4°C in October), leading to very little variation in the difference in temperature between sea and air (ΔT) (summer ΔT of 3.7 \pm 1.4°C SD, winter ΔT 3.6 \pm 0.6°C SD, Wilcoxon test: $W = 827$, $p = 0.174$). There was also no difference in the percentage of time spent in passive flight (taken as the time spent both soaring and gliding) between seasons (12.0 \pm 8.7 and 13.4 \pm 6.9 for summer and winter respectively, Wilcoxon test: $W = 573$, $p = 0.1912$).

Birds used passive flight for periods of 0.2–204 min trip⁻¹ (Fig. 1), which represented a mean of 13% (maximum 34%) of their flight time (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m14410_supp.pdf). Individual thermal climbs lasted for 16 to 212 s (mean 31.5 s). Tropicbirds mostly flew within 100 m of sea level (Fig. 3) with one individual reaching a maximum of 699 m altitude. Peaks in flight height tended to occur near the end of the foraging trips, particularly for birds returning to the colony with a tailwind (Fig. 3).

Thermal soaring was mostly composed of passive circling, but birds flapped during 16 \pm 33% (mean \pm SD, Fig. S1B) of the time spent circling. Birds climbed at a mean rate of 0.56 m s⁻¹ while circling in thermals, but the climb rate varied according to whether or not birds flapped, with flapping increasing the climb rate from 0.57 to 0.84 m s⁻¹ on average (Wilcoxon test: $W = 7349$, $p < 0.001$, $n = 309$). Birds also used both flapping and gliding flight when moving between successive thermal updrafts (Fig. 1).

Birds foraged in different directions from Round Island, according to the nest location. This affected whether they experienced a tailwind on the outbound or return leg of the trip (Fig. S2), with birds tagged at the main study site experiencing the strongest tailwinds in the last portion of the trip, when returning to the colony. Soaring appeared most likely when birds experienced tailwinds, independently of whether this was at the beginning or the end of the flight (Fig. 4). A GLMM confirmed that birds were more likely to switch to soaring–gliding flight with higher ΔT (Fig. S3) and TWC (Table 1), although the marginal r-squared of the model was low ($R^2_m = 0.04$), showing that ΔT and TWC explained little of the variability compared to the random factors ($R^2_c = 0.31$). It was difficult to assess the effect of time of day on the time spent soaring, as most of our study birds were returning to the colony with a tailwind when the proportion of soaring flight peaked (Fig. S4).

Tropicbirds undertook an average of 8.2 preypursuits per trip. The mean altitude of tropicbirds in the minute before a pursuit was 41 \pm 26 m (SD). Com-

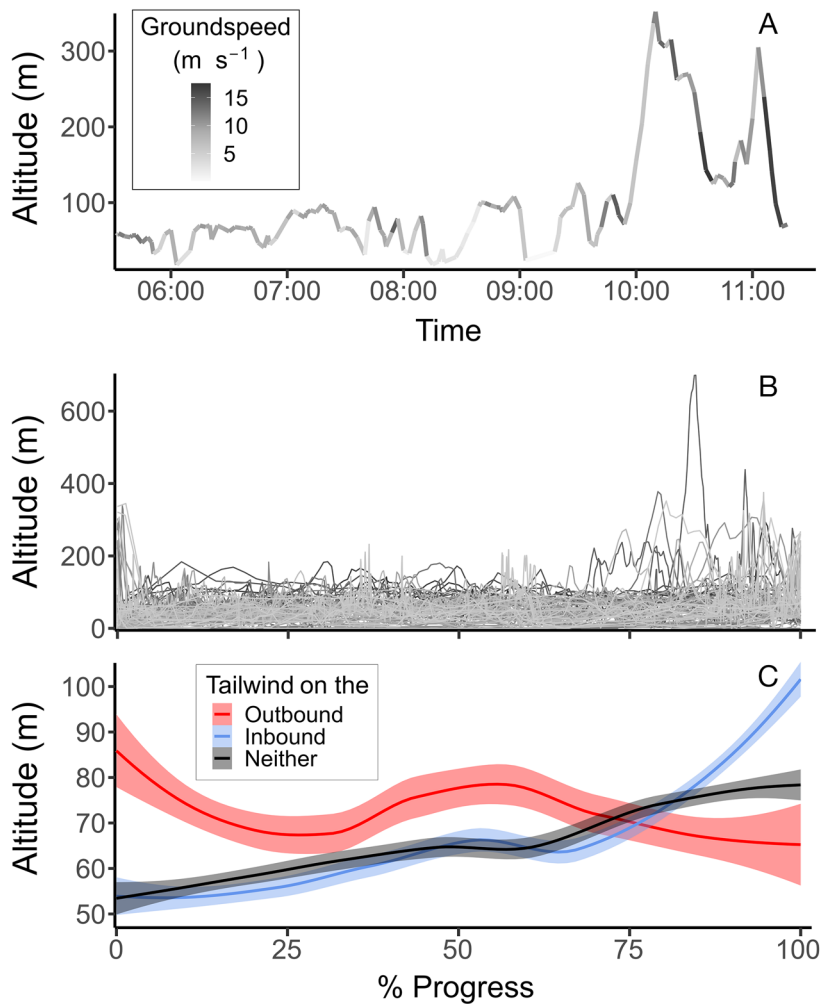


Fig. 3. Altitude profiles of tropicbirds through their foraging trips. (A) Flight altitude during one foraging trip showing that the return to the colony was preceded by increases in flight altitude and subsequently in groundspeed (shown in greyscale). (B) Altitude profiles of all trips. (C) Locally estimated scatterplot smoothing (loess) of altitude according to whether birds experienced a tailwind (mean TWC > 0) only in the outbound (red, $n = 8$) or inbound (blue, $n = 21$) phases of the trip, or neither outbound nor inbound (black). Two trips had a tailwind during both inbound and outbound phases, and these were split, with the first and last 50% of the trips being allocated to the groups with tailwind during the outbound and inbound, respectively

binning these figures, we estimate that tropicbirds climbed 328 m per trip on average in association with feeding behaviour. In general, birds tended to forage less at the beginning and end of their trips, consistent with these periods representing commuting (Fig. 4). The relationship between the use of thermal soaring and the number of pursuits varied depending on whether the birds experienced a tailwind on their outbound or return leg. Birds that experienced a tailwind on their outbound journey had the highest number of prey pursuits roughly 1/3 of the way through their trips, when the proportion of thermal

soaring was also at its highest (Fig. 4). Birds returning to the colony with a tailwind, or with no consistent head or tailwind, used more thermal soaring near the end of the trip, when there were fewer aerial pursuits (Fig. 4).

Groundspeed increased with increasing tailwind for both level flapping flight and soaring–gliding flight (Table 2, Fig. 5). Flapping flight was faster than passive flight for all values of TWC except strong headwinds, where very few instances of passive flight occurred.

Birds were less likely to flap during a soaring bout with increasing tailwind (estimate = -0.3). There was no relationship between the likelihood of flapping within circling, ΔT or body mass (Table 3).

3.2. Capacity for thermal soaring across species

Wing loading increases with body mass, as indicated by the allometric regression line (Fig. 6A). Nonetheless, the seabird species for which we were able to obtain data tended to have low wing loading relative to their body mass, as the species-specific values of wing loading mostly fell below the allometric line (including for frigate birds, terns and even boobies) (Fig. 6A). The wing loading of tropicbirds was very close to that predicted by the allometric scaling relationship. The ability to soar in thermals over the ocean will be influenced by the minimum sink rate during gliding flight.

All species apart from the 3 auks (Atlantic puffin *Fratercula arctica*, common guillemot *Uria algae* and razorbill *Alca torda*) had minimum sink rates $< 0.56 \text{ m s}^{-1}$ (Fig. 6B; Table S2).

4. DISCUSSION

4.1. Behavioural context of thermal soaring

Magnetometry data revealed that red-tailed tropicbirds used extensive periods of thermal soaring and

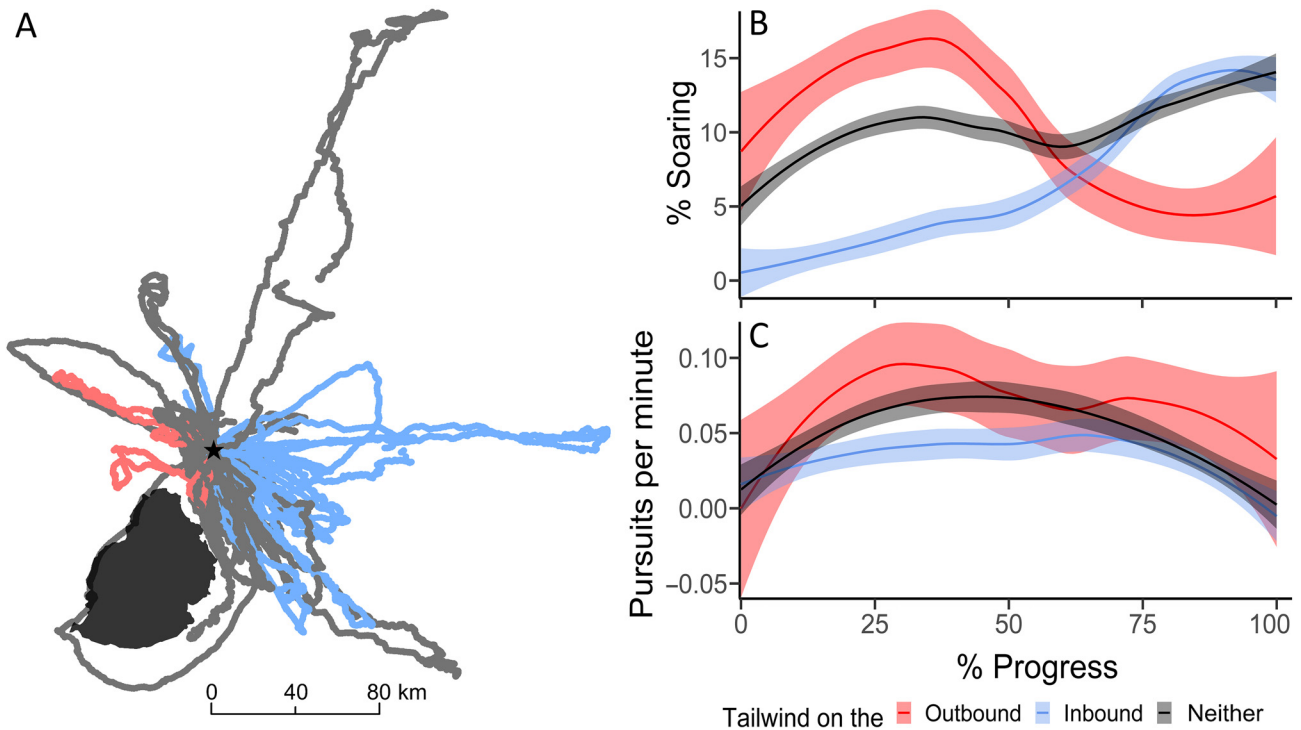


Fig. 4. Occurrence of soaring throughout the foraging trips. (A) Birds foraging to the southeast of the colony experienced a tailwind during the inbound portion of their flight (blue line), while birds foraging to the north of the colony experienced a tailwind during their outbound flight (red line), others experienced no particular pattern of tailwind during their trip (black line). (B) Proportion of time spent soaring (%) in relation to time through the trip. Lines (with 95% confidence intervals) show the smooth loess of flight variables for birds foraging in different directions from the island. (C) Smooth loess of the number of pursuits per minute (with 95% confidence intervals) in relation to time through the trip

Table 1. Summary statistics of the binomial generalised linear mixed effect model showing the effect of the tailwind component (TWC), thermal strength (ΔT) and their interaction on the presence/absence of soaring sampled for each GPS fix across the 76 foraging trips. $R^2_m = 0.04$, $R^2_c = 0.31$. Significance is indicated as *** $p < 0.001$

	Estimate	SE	Z	p
(Intercept)	0.022	0.131	0.166	0.868
ΔT ($^{\circ}C$)	0.347	0.030	11.428	<0.0001***
TWC ($m\ s^{-1}$)	0.144	0.023	6.321	<0.0001***
Mass (g)	-0.196	0.140	-1.411	0.158

Table 2. Output for the model of groundspeed ($m\ s^{-1}$) in relation to the tailwind component (TWC, $m\ s^{-1}$) for level flapping flight (intercept) and soaring-gliding ($R^2_m = 0.42$, $R^2_c = 0.71$). Significance is indicated as *** $p < 0.001$

	Estimate	SE	Z	p
(Intercept)	10.150	0.227	44.71	<0.0001***
TWC	3.547	0.139	25.51	<0.0001***
Soaring-gliding	-2.685	0.290	-9.23	<0.0001***
Mass	0.320	0.243	1.36	0.175
TWC: Soaring-gliding	-1.790	0.245	-7.31	<0.0001***

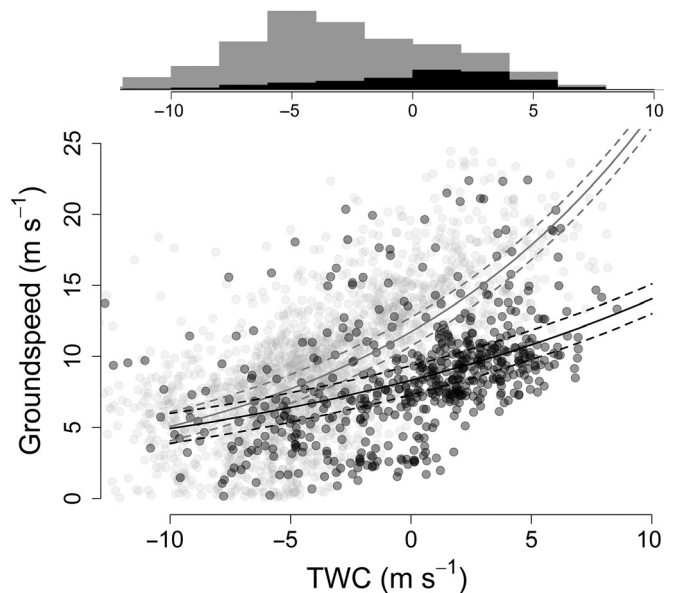


Fig. 5. Groundspeed in relation to the tailwind component (TWC) for level flapping flight (light grey) and soaring-gliding (black). Standard errors of the regressions are represented by the dashed lines. The relative frequencies of passive and flapping flight in relation to the TWC are given in the histogram at the top of the figure

Table 3. Summary statistics of the binomial generalised linear mixed effect model showing the effect of the tailwind component (TWC), thermal strength (ΔT) and body mass on the presence/absence of flapping during a soaring bout. $R^2_m = 0.06$, $R^2_c = 0.33$. Significance is indicated as * $p < 0.05$, ** $p < 0.01$

	Estimate	SE	Z	p
(Intercept)	-0.800	0.264	-3.032	0.002**
TWC (m s^{-1})	-0.373	0.174	-2.152	0.938
ΔT ($^{\circ}\text{C}$)	-0.015	0.188	-0.078	0.031*
Mass (g)	-0.323	0.307	-1.054	0.292

gliding flight in the austral summer and winter, soaring to altitudes up to 699 m. The proportion of the flight time spent soaring (13%) is of a similar magnitude to foraging frigate birds, which are known soaring specialists that spend 27% of their foraging bouts in passive flight (Corbeau et al. 2020). Thermals over the sea therefore appear to represent a valuable resource for tropicbirds, and one that should be available throughout much of their range, which extends east from the Indian Ocean to the Southwest Pacific (<http://datazone.birdlife.org/species/factsheet/red-tailed-tropicbird-phaethon-rubricauda/distribution>).

Thermal soaring is usually used as a strategy for low-cost travel (though insectivores may feed in thermals: de Margerie et al. 2018). Our results suggest that soaring has multiple benefits for red-tailed tropicbirds, occurring during prey-searching, as well as periods with few prey pursuits when it is most likely

used to reduce the cost of transport. Unlike patterns of thermal soaring reported for terrestrial soaring birds (e.g. Williams et al. 2020), tropicbirds frequently flapped when descending between thermal climbs, something that was also reported in ospreys *Pandion haliaetus* crossing the Mediterranean (Duriez et al. 2018). This sometimes preceded prey pursuits, suggesting that birds were increasing their speed in response to feeding opportunities (Fig. 1). Flapping during descending flight could also be compatible with an energy-saving strategy during commuting, as a recent theoretical study by Sachs (2022) showed that alternating phases of ‘powered-gliding’ and climbing flight yielded the lowest fuel consumption per unit distance when compared with other travel flight modes, including flight at a constant altitude. A reduction in cost of transport may be particularly beneficial on the return leg, when the costs of flapping flight are increased by the mass of the prey carried (Sato et al. 2008). Nonetheless, tropicbirds also used thermal soaring to climb between prey pursuits, which occurred throughout much of the foraging trip. Gaining altitude ‘passively’ in thermals offers notable energy savings for birds that search for prey from height, repeatedly descending to the sea surface during prey pursuit and capture, as climbing flight is particularly costly (Berg & Biewener 2008).

Tropicbirds also used thermal updrafts to gain height for other reasons, sometimes climbing to several hundred metres at the end of their trip and then descending rapidly to the colony, particularly when

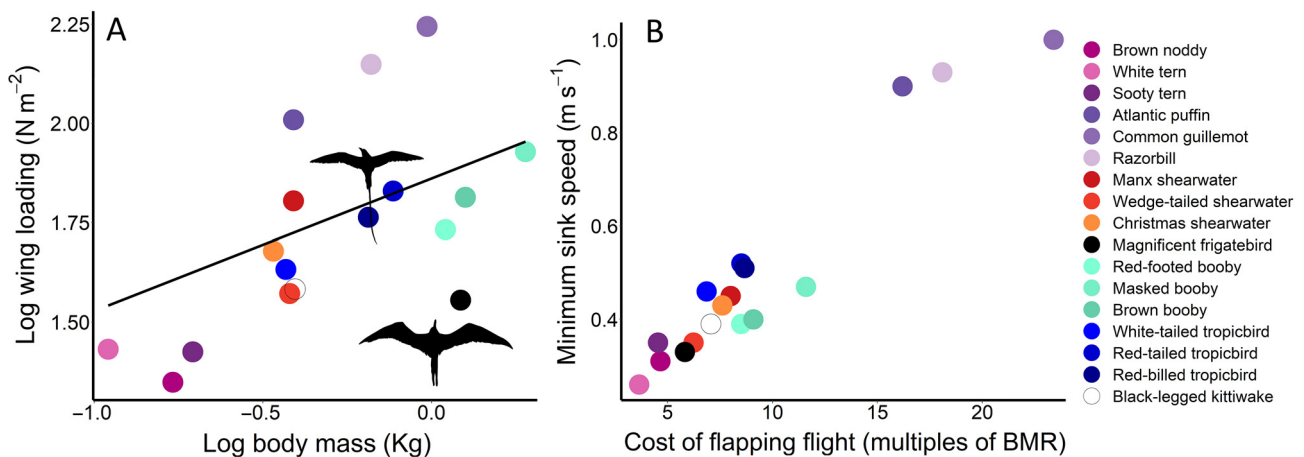


Fig. 6. (A) Wing loading for a range of seabird species in relation to body mass. The black line indicates the allometric line, based on data from 220 species (Pennycuik 2008). (B) Minimum sink rate in gliding flight (which determines the ability to gain altitude in weak thermals) is given in relation to the relative cost of powered flight (given as multiples of the basal metabolic rate [BMR], which relates to the metabolic incentive to switch from flapping to soaring). The largest silhouette indicates the magnificent frigatebird *Fregata magnificens*; the smaller silhouette is nearest the red-tailed tropicbird point. These are the species known to use thermal soaring

experiencing tailwinds (Fig. 3). This could be a defence against potential kleptoparasitism by frigate birds (Le Corre & Jouventin 1997), as red-footed boobies *Sula sula* are less likely to be chased by frigate birds when flying >50 m or after dusk (Le Corre & Jouventin 1997). Indeed, red-footed boobies also ascend up to 500 m during the final phase of their foraging flights, which likely helps them avoid attacks by frigate birds along the coast (Weimerskirch et al. 2005). However, frigate birds were hunted to extinction in the Mascarenes, being recorded on/near Round Island up until 1860 (Weimerskirch et al. 2005) and now only occurring as vagrants. This suggests that tropicbirds increase their arrival altitude in the absence of an immediate threat. In support of this, studies in other taxa have shown that the landscape of fear can affect behaviour decades after predators have disappeared from an area (Laundré et al. 2001).

The key advantage of thermal soaring is that it allows animals to reduce their use of flapping flight. Nonetheless, we found that tropicbirds still flapped while gaining altitude in thermal updrafts, suggesting that these birds may have needed to flap to maintain their position within the narrow thermal core where the upward component is strongest (Williams et al. 2018). Flapping within thermal climbs has only been reported in ospreys (Duriez et al. 2018), suggesting that it is seldom necessary for specialist soaring birds (e.g. Williams et al. 2020). For tropicbirds, thermal climbs appeared to fall into 2 categories, containing little flapping or regular flapping. Intriguingly, birds soaring with a tailwind also flapped less in thermal climbs, suggesting that the wind direction affects the efficiency of turning within a thermal.

4.2. Potential use of thermal soaring across taxa

Our results demonstrate that thermal soaring is not confined to seabirds with morphological adaptations for this flight style, as tropicbirds have an average wing loading for their body mass. Indeed, the comparison of wing loading and sink rates across a range of seabird morphologies suggests that thermal soaring may be more common than generally assumed. We estimate that tropicbirds experienced a mean thermal strength of 0.98 m s^{-1} (adding the birds' sink rate of 0.42 m s^{-1} [Table S2] to the mean climb rate of 0.56 m s^{-1}), which is fairly typical for thermals over the ocean (Weimerskirch et al. 2016). Birds with a minimum sink rate $>1 \text{ m s}^{-1}$, such as auks, will therefore not be able to climb within sea thermals, despite

having strong metabolic motivation to switch from flapping to gliding flight. However, species with sink rates $<1 \text{ m s}^{-1}$ should be able to climb within thermals over the ocean, assuming their flight speeds (and hence turn radii) are low enough to enable them to circle within the strongest part of the uplift (Penny-cuick 1983). Terns, which have lower sink rates and glide speeds than tropicbirds, should also be well equipped to exploit thermals over the ocean (Fig. 6). Black-legged kittiwakes *Rissa tridactyla* have a lower wing loading and sink rate than red-tailed tropicbirds, but similar flight speeds, and larger larvae such as lesser black-backed gulls *Larus fuscus* and herring gulls *L. argentatus* are known to use thermal soaring over the ocean (van Erp et al. 2023 in this Theme Section). Red-footed and brown boobies have similar performance characteristics to red-tailed tropicbirds, in terms of minimum sink rates and glide speeds, and may also be able to use thermal soaring (Weimerskirch et al. 2005). Terns and boobies are also pursuit divers and could potentially use thermal updrafts to reduce the costs of climbing flight required for prey-searching and pursuit. The wing loading of red-tailed tropicbirds is also similar to Manx shearwaters *Puffinus puffinus* and greater than wedge-tailed and Christmas shearwaters *P. pacificus* and *P. nativitatis*. Nonetheless, high-frequency GPS tracks from dynamic soaring species show no evidence of thermal soaring (Gibb et al. 2017).

The fact that frigate birds and gulls are the only seabird species recorded using thermals over the ocean (Weimerskirch et al. 2016, Sage 2022) highlights that high-frequency movement data from magnetometers (often recorded with sub-second resolution; Wilson et al. 2008), high-frequency GPS (e.g. 1 Hz) or radar are required to document this behaviour at sea (cf. Duriez et al. 2018). While altimeters and accelerometers can identify when birds gain height without flapping, they cannot provide insight into whether this is achieved using thermal updrafts or some aspect of the wind field.

4.3. Role of currency in determining the use of thermal soaring

Given that tropicbirds do soar in thermals, and have the flexibility to use this during commuting or prey-searching, why do they not use passive flight more? Thermal soaring was more likely to occur when birds were flying with tailwind assistance, but several trips barely included any soaring, despite

featuring tailwinds and relatively high climb rates. The predominance of powered flight suggests that overall, flight mode is driven by the need for greater speed, rather than energetic efficiency (Shepard et al. 2009). Indeed, birds generally fly faster when feeding young (Norberg 1981), and tropicbirds favour short trips and reduce their resting time during the chick-feeding period to increase the rate of food delivery (Sommerfeld & Hennicke 2010). It is well established that the stereotypical form of thermal soaring flight, with birds gaining altitude in thermals and gliding between them, generally results in lower overall groundspeeds compared to powered flight (Hedenström & Ålerstam 1995). In this study, passive flight (soaring and gliding combined) was consistently slower than flapping flight. The groundspeeds of both flight modes increased with the TWC (potentially explaining why birds switched to soaring more in a tailwind), but even with a 5 m s^{-1} tailwind, tropicbirds were able to fly some 7 m s^{-1} faster when flapping. The groundspeeds of the 2 modes were predicted to converge in stronger headwinds, but this was likely an artefact of having very few instances of soaring in strong headwinds.

The use of soaring flight may increase outside the breeding season when time constraints are relaxed and birds are free to select their flight direction in relation to prey availability and the wind, rather than being constrained by the need to return to a central place (the breeding colony) (Weimerskirch et al. 2016). Thermals over the ocean should be available year-round in regions such as the Indian Ocean (Weimerskirch et al. 2016), yet we know very little about the extent to which they are used outside the breeding season, as high-frequency loggers are typically only deployed during breeding. The notable exception here is frigate birds, where thermal soaring increased from 27 to 82% of their flight time between the breeding season and migration (Corbeau et al. 2020). This demonstrates the impact that a change in currency can have on flight behaviour and energetics, as priorities shift from time minimisation to energy minimisation. Models of flight costs outside the breeding season that assume birds are always flapping may therefore over-estimate flight costs by a substantial margin where they are based on the exclusive use of flapping flight. Further high-frequency movement data should provide insight into the taxa that use thermal soaring, how this varies throughout the annual cycle, as well as the wider role of thermal soaring in structuring year-round movement decisions (cf. Weimerskirch et al. 2016, Nourani et al. 2021).

Data availability. The data sets generated and/or analysed during the current study are available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.251> (Garde et al. 2022).

Acknowledgements. This work was funded by a European Research Council starter grant (715874 to E.L.C.S.), under the European Union's Horizon 2020 Research and Innovation program. Preliminary fieldwork was conducted with funding from Swansea University. We are grateful to the National Parks and Conservation Service, Government of Mauritius, who provided permission to access Round Island. This work was part of B.G.'s PhD thesis entitled 'Fine scale changes in flight effort revealed by animal borne loggers', awarded by Swansea University.

LITERATURE CITED

- Barton K (2015) Package 'MuMIn'. R package version 1.47.1. <https://CRAN.R-project.org/web/packages/MuMIn/index.html>
- ✦ Becciu P, Rotics S, Horvitz N, Kaatz M and others (2020) Causes and consequences of facultative sea crossing in a soaring migrant. *Funct Ecol* 34:840–852
- ✦ Berg AM, Biewener AA (2008) Kinematics and power requirements of ascending and descending flight in the pigeon (*Columba livia*). *J Exp Biol* 211:1120–1130
- Bradbury T (1989) *Meteorology and flight: a pilot's guide to weather*. A&C Black, London
- ✦ Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400
- ✦ Corbeau A, Prudor A, Kato A, Weimerskirch H (2020) Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. *J Anim Ecol* 89: 20–28
- ✦ de Margerie E, Pichot C, Benhamou S (2018) Volume-concentrated searching by an aerial insectivore, the common swift, *Apus apus*. *Anim Behav* 136:159–172
- ✦ Duriez O, Peron G, Gremillet D, Sforzi A, Monti F (2018) Migrating ospreys use thermal uplift over the open sea. *Biol Lett* 14:20180687
- ✦ Gajda J, Wyłomańska A (2015) Time-changed Ornstein–Uhlenbeck process. *J Phys A Math Theor* 48:135004
- ✦ Garde B, Fell A, Krishnan K, Jones CG and others (2022) Data from: Thermal soaring in tropicbirds suggests that diverse seabirds may use this strategy to reduce flight costs. Movebank Data Repository. <https://doi.org/10.5441/001/1.251>
- ✦ Gardner AS, Duck CD, Greig S (1985) Breeding of the Trindade petrel *Pterodroma arminjoniana* on Round Island, Mauritius. *Ibis* 127:517–522
- ✦ Gibb R, Shoji A, Fayet al. Perrins CM, Guilford T, Freeman R (2017) Remotely sensed wind speed predicts soaring behaviour in a wide-ranging pelagic seabird. *J R Soc Interface* 14:20170262
- ✦ Gunner RM, Holton MD, Scantlebury DM, Hopkins P and others (2021a) How often should dead-reckoned animal movement paths be corrected for drift? *Anim Biotelemetry* 9:43
- ✦ Gunner RM, Holton MD, Scantlebury MD, van Schalkwyk OL and others (2021b) Dead-reckoning animal move-

- ments in R: a reappraisal using GundoG.Tracks. *Anim Biotelemetry* 9:23
- Harel R, Horvitz N, Nathan R (2016) Adult vultures outperform juveniles in challenging thermal soaring conditions. *Sci Rep* 6:27865
- Hartig F (2017) DHARMA: residual diagnostics for hierarchical (multi-level mixed) regression models. R package version 0.4.6. <https://CRAN.R-project.org/web/packages/DHARMA/index.html>
- Hedenström A, Ålerstam T (1995) Optimal flight speed of birds. *Philos Trans R Soc Lond B Biol Sci* 348:471–487
- Hertel F, Ballance LT (1999) Wing ecomorphology of seabirds from Johnston Atoll. *Condor* 101:549–556
- Klein Heerenbrink M, Johansson L, Hedenström A (2015) Power of the wingbeat: modelling the effects of flapping wings in vertebrate flight. *Proc R Soc A* 471:20140952
- Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Can J Zool* 79:1401–1409
- Le Corre M, Jouventin P (1997) Kleptoparasitism in tropical seabirds: vulnerability and avoidance responses of a host species, the red-footed booby. *Condor* 99:162–168
- Le Corre M, Cherel Y, Lagarde F, Lormée H, Jouventin P (2003) Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird *Phaethon rubricauda*. *Mar Ecol Prog Ser* 255:289–301
- Mandel JT, Bohrer G, Winkler DW, Barber DR, Houston CS, Bildstein KL (2011) Migration path annotation: cross-continental study of migration-flight response to environmental conditions. *Ecol Appl* 21:2258–2268
- Norberg RÅ (1981) Optimal flight speed in birds when feeding young. *J Anim Ecol* 50:473–477
- Nourani E, Vansteelant WM, Byholm P, Safi K (2020) Dynamics of the energy seascape can explain intra-specific variations in sea-crossing behaviour of soaring birds. *Biol Lett* 16:20190797
- Nourani E, Bohrer G, Becciu P, Bierregaard RO and others (2021) The interplay of wind and uplift facilitates over-water flight in facultative soaring birds. *Proc R Soc B* 288:20211603
- Pennycuik CJ (1983) Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentalis* and *Coragyps atratus*. *J Exp Biol* 102:307–325
- Pennycuik CJ (2008) *Modelling the flying bird*. Elsevier, Amsterdam
- R Core Team (2020) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Sachs G (2022) Powered-gliding/climbing flight. *J Theor Biol* 547:111146
- Safi K, Kranstauber B, Weinzierl R, Griffin L and others (2013) Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. *Mov Ecol* 1:4
- Sage E (2022) Wind energy for all!: The dynamic flight of gulls in human-engineered landscapes. PhD thesis, University of Amsterdam
- Sage E, Bouten W, van Dijk W, Camphuysen KC, Shamoun-Baranes J (2022) Built up areas in a wet landscape are stepping stones for soaring flight in a seabird. *Sci Total Environ* 852:157879
- Sapir N, Wikelski M, McCue MD, Pinshow B, Nathan R (2010) Flight modes in migrating European bee-eaters: Heart rate may indicate low metabolic rate during soaring and gliding. *PLOS ONE* 5:e13956
- Sato K, Daunt F, Watanuki Y, Takahashi A, Wanless S (2008) A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *J Exp Biol* 211:58–65
- Scacco M, Flack A, Duriez O, Wikelski M, Safi K (2019) Static landscape features predict uplift locations for soaring birds across Europe. *R Soc Open Sci* 6:181440
- Shamoun-Baranes J, Van Loon E, van Gastere H, van Belle J, Bouten W, Buurma L (2006) A comparative analysis of the influence of weather on the flight altitudes of birds. *Bull Am Meteorol Soc* 87:47–62
- Shamoun-Baranes J, Bouten W, Van Loon EE, Meijer C, Camphuysen C (2016) Flap or soar? How a flight generalist responds to its aerial environment. *Philos Trans R Soc B* 371:20150395
- Shepard EL, Wilson RP, Quintana F, Gomez Laich A, Forman DW (2009) Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proc R Soc B* 276:3149–3155
- Shepard EL, Lambertucci SA, Vallmitjana D, Wilson RP (2011) Energy beyond food: foraging theory informs time spent in thermals by a large soaring bird. *PLOS ONE* 6:e27375
- Solomon S, Qin D, Manning M, Marquis M and others (eds) (2007) *Climate change 2007: the physical science basis*. Working group I contribution to the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge
- Sommerfeld J, Hennicke JC (2010) Comparison of trip duration, activity pattern and diving behaviour by red-tailed tropicbirds (*Phaethon rubricauda*) during incubation and chick-rearing. *Emu* 110:78–86
- Spear LB, Ainley DG (1997) Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* 139:221–233
- Uhm T, Yi S (2021) A comparison of normality testing methods by empirical power and distribution of p-values. *Commun Stat Simul Comput* 52:4445–4458
- van Erp J, Sage E, Bouten W, van Loon E, Camphuysen KC, Shamoun-Baranes J (2023) Thermal soaring over the North Sea and implications for wind farm interactions. *Mar Ecol Prog Ser:WINDav4* <https://doi.org/10.3354/meps14315>
- Vansteelant WM, Shamoun-Baranes J, van Manen W, van Diermen J, Bouten W (2017) Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic Flyway. *J Anim Ecol* 86:179–191
- Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2005) The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proc R Soc B* 272:53–61
- Weimerskirch H, Bishop C, Jeanniard-du-Dot T, Prudor A, Sachs G (2016) Frigate birds track atmospheric conditions over months-long transoceanic flights. *Science* 353:74–78
- Weinzierl R, Bohrer G, Kranstauber B, Fiedler W, Wikelski M, Flack A (2016) Wind estimation based on thermal soaring of birds. *Ecol Evol* 6:8706–8718
- Williams HJ, Duriez O, Holton MD, Dell'Omo G, Wilson RP, Shepard EL (2018) Vultures respond to challenges of near-ground thermal soaring by varying bank angle. *J Exp Biol* 221:jeb174995

- ✦ Williams HJ, Shepard E, Holton MD, Alarcón P, Wilson R, Lambertucci S (2020) Physical limits of flight performance in the heaviest soaring bird. *Proc Natl Acad Sci USA* 117:17884–17890
- ✦ Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endang Species Res* 4:123–137
- Wilson RP, Holton MD, Di Virgilio A, Williams H and others (2018) Give the machine a hand: a Boolean time-based decision-tree template for rapidly finding animal behaviours in multisensor data. *Methods Ecol Evol* 9: 2206–2215
- ✦ Wilson RP, Börger L, Holton MD, Scantlebury DM and others (2020) Estimates for energy expenditure in free-living animals using acceleration proxies: a reappraisal. *J Anim Ecol* 89:161–172
- ✦ Woodcock AH (1975) Thermals over the sea and gull flight behavior. *Boundary-Layer Meteorol* 9:63–68
- ✦ Young IR, Zieger S, Babanin AV (2011) Global trends in wind speed and wave height. *Science* 332:451–455

*Editorial responsibility: Thomas A. Clay (Guest Editor),
Santa Cruz, California, USA*
Reviewed by: 3 anonymous referees

Submitted: November 18, 2022
Accepted: August 11, 2023
Proofs received from author(s): October 16, 2023