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Flap or soar? How a flight generalist responds to its aerial environment

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The aerial environment is heterogeneous in space and time and directly influences the costs of animal flight. Volant animals can reduce these costs by using different flight modes, each with their own benefits and constraints. However, the extent to which animals alter their flight modes in response to environmental conditions has rarely been studied in the wild. To provide insight into how a flight generalist can reduce the energetic cost of movement, we studied flight behaviour in relation to the aerial environmental and landscape using hundreds of hours of global positioning system and triaxial acceleration measurements of the lesser black-backed gull (*Larus fuscus*). Individuals differed largely in the time spent in flight, which increased linearly with the time spent in flight at sea. In general, flapping was used more frequently than more energetically efficient soaring flight. The probability of soaring increased with increasing boundary layer height and time closer to midday, reflecting improved convective conditions supportive of thermal soaring. Other forms of soaring flight were also used, including fine-scale use of orographic lift. We explore the energetic consequences of behavioural adaptations to the aerial environment and underlying landscape and implications for individual energy budgets, foraging ecology and reproductive success.

This article is part of the themed issue 'Moving in a moving medium: new perspectives on flight'.

1. Introduction

Through natural selection, volant animals have evolved a range of physiological and morphological traits, which result in efficient flight [1–4]. Flight efficiency is also strongly influenced by the aerosphere, the aerial environment through which animals travel [5]. As the aerosphere is heterogeneous in space and in time, animals may alter their flight behaviour to take advantage of profitable conditions or avoid adverse ones [6]. Animals respond to atmospheric conditions by selecting when [7,8] or where to fly in three-dimensional space [9–13], by adjusting flight kinematics [14,15] or by altering airspeeds or flight directions [16–18]. Several species of birds and bats reduce flight costs by altering their mode of flight from continuous flapping to intermittent or soaring flight [19–22].

Some avian species have evolved traits to specialize in one particular flight mode [1,23]. For species that have the capacity to use a range of flight modes, an additional behavioural adaptation to environmental variability could be selecting flight modes best suited to the conditions experienced. Gulls (*Laridae*), for example, due to their eco-morphology and intermediate body size, are highly manoeuvrable species that have the ability to radically alter their flight mode in response to external factors such as atmospheric conditions while flying over a broad range of habitats [24–28]. The efficiency of each flight mode in terms of time and energy differs, depending on the motivation for flight (e.g. commuting, migrating, searching for food) and environmental conditions experienced [1,21,29]. Soaring flight is

energetically less costly than flapping flight [26,30,31]. Yet soaring flight, whether supported by thermal convection, orographic lift (air that rises after hitting a topographic obstruction) or vertical wind shear, will be constrained by the availability of appropriate atmospheric conditions [25,32–34]. Horizontal rather than vertical air flow will strongly influence flapping flight costs in the form of time and energy [16,18,29,35].

The propensity of birds to alter flight modes in the wild has rarely been studied in detail for extensive periods of time and over a range of landscapes. Studies have so far only been feasible in very large birds [9,36] or for relatively short periods of time when studying smaller species [37]. It is due to recent developments in tracking technology that researchers can measure movement and behaviour almost continuously, over multiple years and individuals, of smaller species and beyond the range of visual observations. Global positioning system (GPS) tracking that collects information on flight speed, altitude, triaxial acceleration and geographical position, provides a unique opportunity to explore flight behaviour in the context of atmospheric conditions experienced, regardless of the time of day, weather conditions or landscape [38,39]. In this study, we use state-of-the-art tracking technology to quantify the flight behaviour of lesser black-backed gulls (*Larus fuscus*). The aim of this study was to determine the extent to which gulls use different flight modes and how this may be constrained or facilitated by the aerial environment and underlying landscape. To achieve this objective, we modelled the environmental envelope of soaring and flapping flight, defined as the conditions within which a specific flight mode has been observed. This approach provided insight into the energy invested in flight under different environmental conditions and revealed potential consequences for foraging ecology and reproductive success.

We measured behaviour during hundreds of hours of foraging movements of multiple individuals during several breeding seasons. Based on existing knowledge of flight behaviour, the foraging ecology of the study population and boundary layer dynamics, there were several expectations that we explored in this study. (i) We expected that in general, flapping flight would be used more frequently than soaring flight. This is due to the eco-morphology of the species, and because flapping flight would be less constrained by environmental conditions than soaring flight, enabling birds to commute and search for food under a broader range of environmental conditions. (ii) We expected that the propensity to soar would increase with improved thermal convection and we used boundary layer height as a proxy for thermal depth and the convective velocity scale (w^*) as a proxy for the thermal updraught velocity [9,40]. The convective boundary layer generally follows a clear diurnal pattern, wherein thermal depth, thermal diameter and vertical velocity increase after sunrise and then decrease before sunset [40]. We therefore expected a strong association between time of day and the proportion of time spent in soaring flight. Soaring flight, however, might not be limited to convective conditions and gulls were expected to use orographic lift as well as vertical wind shear [41,42]. We therefore expected that, (iii) the propensity to soar would increase with a higher wind gradient or higher wind speeds near the surface, increasing orographic lift in heterogeneous terrain and around anthropogenic structures or supporting non-convective soaring at sea. We discuss how the energetic investment in movement can vary depending on flight mode selection, the underlying landscape, atmospheric conditions at the meso- and micro-scale and potential consequences for different foraging strategies and for reproductive success.

2. Material and methods

(a) Measuring gull movements

Adult lesser black-backed gulls were captured during incubation in a breeding colony (53.009° N, 4.717° E) on the Wadden Sea island Texel, The Netherlands. Birds were fitted with an 18 g UvA-BiTS GPS-tracker [38] using a wing harness [43] made of a Teflon ribbon threaded with a nylon string. Precautions were taken to reduce any negative impact on the birds, and birds were released immediately after tagging, within 20 min of capture. Individuals continued to breed after tagging and a similar study on lesser black-backed gulls using the same harness design found no short-term impacts on reproduction [44]. For details about the tagging procedures and the breeding colony see [45]; for technical details about the tracking system see [38]. Using bidirectional communication between the GPS-tracker and a base station located in the breeding colony, tracking data was remotely downloaded and new measurement schemes were uploaded during the breeding season. The same individual could be tracked over multiple years, but birds had to return to the colony for remote download of the data. We used tracking data collected between 15 May and 14 June 2012, 2013 and 2014. This period was chosen in order to compare flight for a part of the breeding season when birds exhibited central place foraging and had a strong bond to the breeding colony regardless of their breeding status [45]. This enabled us to collect relatively high resolution GPS data as well as triaxial acceleration data needed for this study without the risk of filling the on-board memory. GPS measurements were taken every 5 min when birds left the colony, higher resolution measurements (e.g. every 3–30 s) were taken on occasion, and lower measurement frequencies of 10–20 min were used when battery power was low. Triaxial acceleration, with surge (x), sway (y) and heave (z), was periodically measured at 20 Hz for 1–3 s, directly following a GPS fix. Only birds with triaxial acceleration measurements were included in this study.

(b) Classifying gull activity

We defined 10 activity classes, which are described in the electronic supplementary material, table S1. Using expert interpretation of the data, based on the GPS location, track geometry, the triaxial acceleration and examination of several video recordings made simultaneously with accelerometer measurements (see e.g. electronic supplementary material, video S1; video S1 in [46]), 1 s tri-axial acceleration segments were assigned to one of the 10 activity classes. To select data for behavioural annotation, a random sample of 28 was taken from a sampling frame containing unique combinations of individual bird and date (bird–date), resulting in data selected from 28 measurement days and 14 individuals. For each bird–date combination, five accelerometer segments were annotated and then 20 segments were skipped, and this procedure was repeated for the entire bird-day. In total 3505 segments of 1 s were annotated.

From the tracking data, we calculated 37 data features (electronic supplementary material, table S2) that could be used for behavioural classification. In order to select a robust set of predictive features, we went through three steps to reduce the number of features. We made 10 random selections of 40% of the annotated data and trained a decision tree on each dataset using the C4.5 machine learning algorithm [47]. From each tree we selected the features that appeared in the top four nodes and retained these features from all 10 trees; all other features were removed from further analysis. Using this subset of features, we repeated this procedure twice, each time retaining a subset of the features. Throughout the modelling, the overall classification error was used as the criterion to be minimized, weighing all activity classes based on their occurrences. This procedure resulted in a set of 14 features that were used to build a random forest classifier. A random forest classifier with 50 trees

was trained [48] using the final set of 14 features and a random subset of 70% of the annotated data. The resulting model was then validated on the remaining 30% of the data. This resulting model was then applied to all unclassified data. Annotation and classification were conducted using software developed in collaboration with the Netherlands eScience Center [49,50]. We used the decision tree and the random forest classifiers from WEKA (Waikato Environment for Knowledge Analysis) datamining software [51].

(c) Data processing and environmental annotation

The GPS locations that were annotated with activity classes in the previous steps were resampled to 5 min intervals, as this was the measurement interval most commonly used. We felt this would provide a more even distribution of our data and achieve the right balance between the resolution of the interpolated environmental data and the aim to retain a large sample of bird flight behaviour observations. We further filtered the data to exclude any locations that were less than 150 m from the centre of the colony in order to represent flight behaviour outside the colony (for details, see [45]). All GPS locations were then assigned a class of land or sea based on a 1 km resolution land–sea mask raster (ESRI Ocean Mask World 1 km); data integration was conducted in arcMAP.

To acquire and derive the atmospheric variables of interest, we used the ERA-Interim dataset [52] produced by ECMWF (European Centre for Medium-Range Weather Forecasts). The dataset has a spatial resolution of approximately 80 km, and temporal resolution 3 h. We extracted u and v wind components (m s^{-1}) at 10 m and 1000 mb (111 m based on the International Standard Atmosphere [ISA] conditions), temperature at 1000 mb (K), geopotential height at 1000 mb (m), surface sensible heat flux (W m^{-2}) and boundary layer height, blh (m). A larger boundary layer height generally indicates better convective conditions for soaring flight [40,53]. As flight altitudes were generally low (median = 16 m, 95% below 227 m above surface level), we focused on meteorological variables close to the surface. We annotated the GPS tracking data with meteorological parameters by selecting the meteorological grid cell closest in space and time to each GPS measurement.

To provide a proxy of the thermal updraught velocity, we calculated the convective velocity scale, w^* [9,40] (equation (2.1)).

$$w^* = \left(\frac{g z}{T} \cdot \frac{H}{\rho C_p} \right)^{1/3}, \quad (2.1)$$

where g = gravitational acceleration (m s^{-2}), z = boundary layer height (m), T = potential temperature (K) and H = surface sensible heat flux (W m^{-2}), ρ = density of air according to ISA (kg m^{-3}), C_p = specific heat of air ($\text{J kg}^{-1} \text{K}^{-1}$).

We calculated the wind speed (V_w) at 10 m and at 1000 mb and subsequently calculated the wind speed gradient (equation (2.2)). If the altitude at 1000 mb was less than 11 m, the values were considered unreliable and removed from the dataset.

$$\Delta V_w = \frac{V_{w2} - V_{w1}}{h - 10}, \quad (2.2)$$

where V_{w1} = wind speed at 10 m, V_{w2} = wind speed at 1000 mb and h = geopotential height at 1000 mb.

Records were removed from the dataset if any of the following variables were not available: blh, V_w (10 m), w^* , ΔV_w ; this resulted in a dataset with 89 755 records to calculate the proportion of time spent in flight and 18 656 records of soaring and flapping flight. Instantaneous airspeed was calculated using vector summation and based on instantaneous ground speed measured by the GPS and wind speed at 10 m.

(d) Summary statistics of flight

For our subsequent analysis, we merged extreme flapping (ExFlap) with flapping flight (Flap) as this was a very small aspect and was

considered a subset of flapping flight. Once we had compiled a dataset including flight parameters and environmental conditions, we calculated a range of summary statistics related to flight. Our study included data from 18 individuals, several of which were tracked over multiple years, resulting in 35 bird–year combinations (electronic supplementary material, table S3). For each bird–year, we calculated the percentage of time spent in flight, % flapping, % soaring, % mixed flight, % flight over sea, % flight over land, % flapping and % soaring over land or sea. Percentages were calculated by dividing the number of records in a specific category (e.g. flapping flight) by the sum of all records for that bird–year and multiplying the quotient by 100 (e.g. (flapping flight records/all records) \times 100). Furthermore, we calculated the percentage of flight time spent soaring ((soar records/flight records) \times 100). We provide the mean instantaneous airspeeds and ground speeds for each flight mode as these are informative when considering flight energetics. The mean \pm s.d. as well as the coefficient of variation (CV) are provided for all flight parameters across all bird–years. For comparison of measured airspeeds with estimated airspeeds based on aerodynamic theory, we calculated V_{bg} (airspeed at best glide ratio) and $V_{cc(max)}$ (maximum cross-country airspeed at climb rate = 1 ms^{-1}) for comparison with soaring flight, and V_{mp} (minimum power airspeed during flapping flight) and V_{mr} (maximum range airspeed) for comparison with flapping flight assuming a flight altitude of 16 m above surface level and using morphological parameters provided in the flight database (body mass = 0.806 kg, wing area = 0.191 m^2 , wing-span = 1.34 m, aspect ratio = 9.42) [34].

(e) Modelling the environmental envelope of soaring and flapping

Our aim was to model the environmental envelope of soaring and flapping flight, at opposite ends of a continuum of flight mode and wing kinematics [54]. We therefore excluded the class mixed flight from this part of the analysis as it represented intermittent flight modes including flap-gliding as well as an intermediate form of soaring. We used generalized linear mixed models with a logit link function and a binomial error distribution to model the probability of soaring flight. Individuals were included as random factors for the intercept. We used blh, V_w (at 10 m), w^* , ΔV_w and time of day as predictors. Time of day was included as it provides a generalized representation of the diurnal development of the boundary layer. Preliminary exploration of flight mode in relation to time of day showed a clear daily change in the proportion of time spent soaring which reached a peak at about 12.00 UTC (electronic supplementary material, figure S1). In order to derive a linear variable that could represent this general diurnal pattern we calculated 'hourR' the absolute value of 12.00 UTC minus the time of day of the flight measurement. Data from the years 2012 and 2013 were used as a training set during model fitting ($n = 12\,365$ GPS fixes with behavioural annotation). Models were then validated using data from 2014 ($n = 6291$). All variable combinations (additive models only) were tested during model training and validation, which led to 32 different models. Once models were fit they were evaluated based on two criteria: parameter significance and AUC (area under the receiver operating characteristic curve) value. The AUC values were compared and models belonging to the upper 25% percentile were selected. From these models, only those with significant predictors (0.05 level of significance) were retained to be further described and interpreted. This description comprised the summary of model coefficients and calculation of the overall error rate in the calibration and validation datasets, using a classification threshold that maximized the overall correct prediction rate in the calibration dataset. The interpretation consisted of visually checking the model-error over a range of predictor variables in

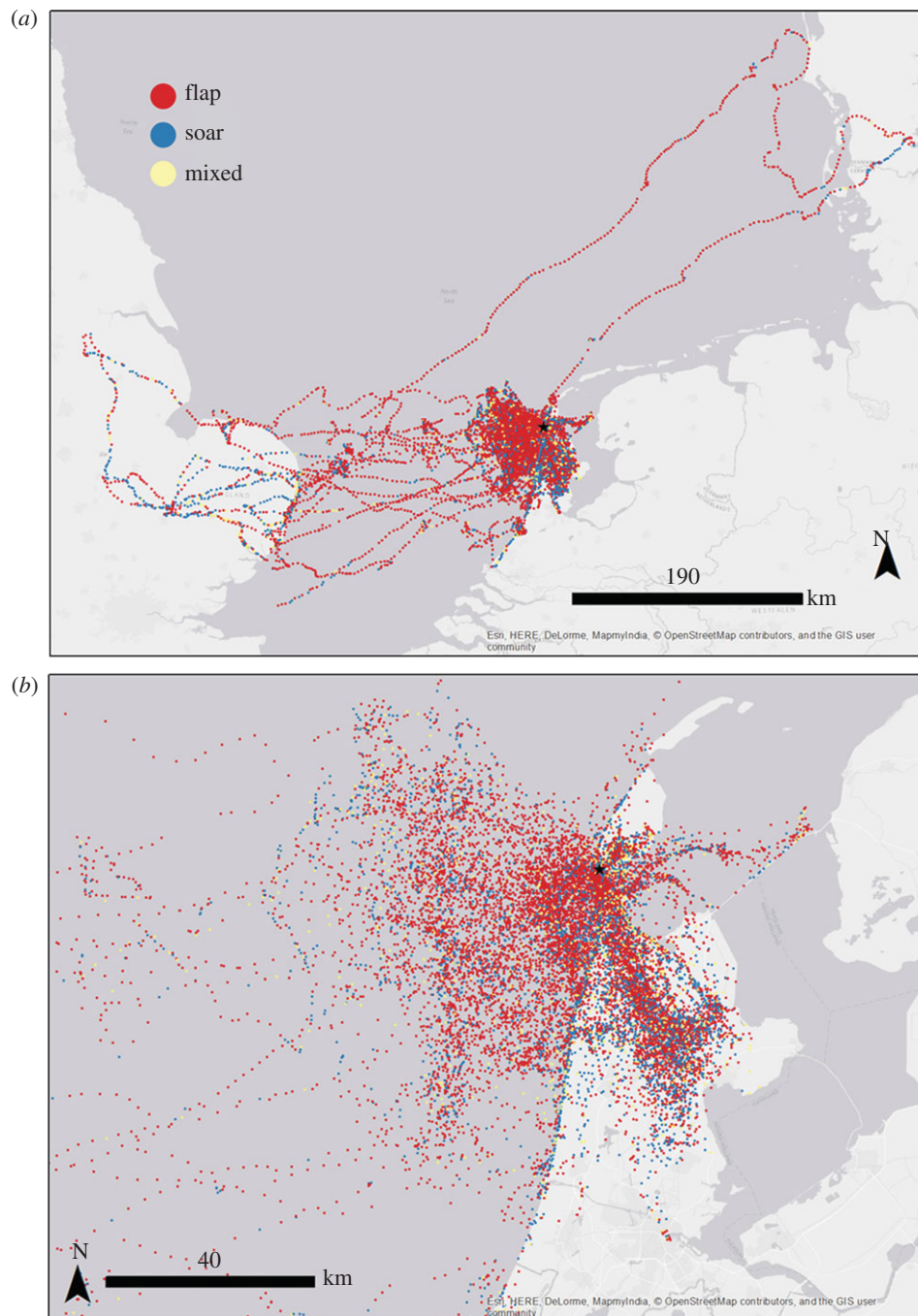


Figure 1. Spatial distribution of flight measurements. (a) Full spatial range of measurements from 15 May to 14 June including (b) measurements in and around the breeding colony. Each point is a measurement resampled to every 5 min, for all bird–years. Red, blue and yellow indicate flapping, soaring and mixed-flight modes, respectively (see colour scheme in panel (a)). The location of the breeding colony on Texel is indicated with a black star. The World Light Grey Base Map provided via the ArcGIS Map service is used as a base layer.

both calibration and validation datasets and relating the model coefficients to what is expected on the basis of physical and biological understanding.

3. Results

Electronic supplementary material, table S3, provides an overview of the flight behaviour per individual and year (bird–year). When outside the colony, gulls spent $30.6 \pm 15.3\%$ of their time in flight (range 7.6–64.1%, CV = 0.5). As expected, all birds spent more time flapping than soaring. The percentage of flight time spent soaring was 26.9% and

less variable across individuals than the percentage of time spent in flight (CV = 0.3). Birds used flapping, soaring and mixed-flight modes over land and sea (figure 1; electronic supplementary material, table S3). Over land, soaring was observed predominantly along the coastal dunes, but also inland (figure 1b). The percentage of time spent in flight over land ($12.4 \pm 8.7\%$) or sea ($18.2 \pm 16.5\%$) varied considerably between individuals. Furthermore, the percentage of time spent in flight increased linearly with percentage of time in flight at sea (weighted linear regression based on sample size per bird–year $y = 0.83x + 14.33$, $R^2 = 0.84$, $p < 0.001$, $n = 35$). Mean ground speed and airspeed during soaring was lower than during flapping and airspeeds were higher than ground

speeds for all flight modes (electronic supplementary material, figure S2). Mean airspeed during flapping flight ($11.9 \pm 1.3 \text{ ms}^{-1}$) was very similar to estimated minimum power speed ($V_{\text{mp}} = 11.4 \text{ ms}^{-1}$) and mean airspeed during soaring flight ($10.5 \pm 1.1 \text{ ms}^{-1}$) was very similar to V_{bg} but much higher than $V_{\text{cc(max)}}$ ($V_{\text{bg}} = 9.9 \text{ ms}^{-1}$, $V_{\text{cc(max)}} = 7.4 \text{ ms}^{-1}$).

As expected, when data were aggregated for all bird-years, the proportion of time spent soaring increased with increasing boundary layer height (electronic supplementary material, figure S1). The proportion of time spent soaring was highest around 12 UTC, decreasing before and after 12.00 and stabilizing at relatively low levels at night between 20.00 and 05.00 UTC (electronic supplementary material, figure S1). The lack of variation in proportion of time spent soaring at night corresponded to the time when the mixed boundary layer generally collapses and becomes stable. The probability of soaring was higher with positive values of w^* than negative values; however, there was a large overlap in the range of wind speeds and wind gradients in which flapping and soaring were observed (electronic supplementary material, figure S3).

Two models met the selection criteria (within the 25 percentile range of models with highest AUC; and all predictors significant). The first included boundary layer height (blh in km), time from 12.00 (hourR) and wind speed at 10 m (V_w , m s^{-1}) (electronic supplementary material, table S4). The second model included blh and hourR. These models had the following functional forms (equations (3.1a) and (3.1b)):

$$p = \frac{1}{1 + e^{-(b - 0.14\text{hourR} + 0.68\text{blh} + 0.02V_w)}} \quad (3.1a)$$

and

$$p = \frac{1}{1 + e^{-(b - 0.14\text{hourR} + 0.68\text{blh})}} \quad (3.1b)$$

with p the probability that a bird is soaring (p closer to unity) or flapping (p closer to zero) and b as a random factor which differs per bird. As may be expected given the very similar parameter values, the two models had similar performance statistics. As the simpler model (3.1b) performed slightly better on the validation data, we will further report the properties of this model. The intercept (mean \pm s.d.) was -0.58 ± 0.31 , with an AUC-value on the validation data of 0.69 (0.95 CI: 0.68–0.70). When selecting a threshold that maximizes the proportion of correct prediction ($p = 0.47$), it had an overall correct prediction rate of 0.71 for the calibration and 0.73 for the validation datasets. A visual assessment showed that the model error was homogeneous over the range hourR (0–12 h) and blh (0–1.9 km). The probability of soaring increased with increasing boundary layer height and decreased with time from 12.00 UTC, and thus was highest around 12.00 UTC. When comparing the parameter space for these two main predictors, the environmental envelope where soaring is most prominent is clearly shifted in space from flapping flight (figure 2), with soaring most prominent when the boundary layer was relatively deep and time of day is close to 12.00 UTC. The area of overlap between soaring and flapping flight when the boundary layer is shallow probably represents non-convective soaring. From this generalized perspective based on mesoscale parameters, it appears that boundary layer height and time of day, both reflecting thermal convection,

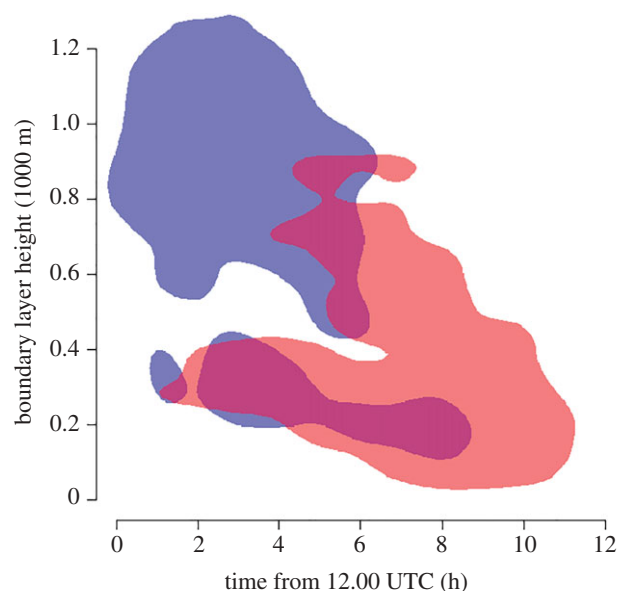


Figure 2. Environmental envelope of soaring and flapping flight. Using a kernel density estimator, we show the 50 percentile for soaring (blue) and flapping flight (red) calculated independently for each flight mode across the two main environmental predictors boundary layer height (blh (km), y-axis) and time from 12.00 UTC (hour (h), x-axis).

are the predominant factors influencing the probability of birds selecting soaring flight.

The model clearly reflected the importance of thermal convection for soaring; however, contrary to our expectations factors such as w^* reflecting thermal updraught velocity supporting thermal soaring, or wind speed gradient that would support other forms of soaring, did not have a statistically significant impact on the probability of soaring. Note however, that in the first model (equation (3.1a)) wind speed had a positive influence on the probability of soaring, probably due to the importance of wind speed for generating orographic lift as well as soaring based on wind shear. To gain further insight into fine-scale decision making during flight and the potential importance of orographic lift not covered in our modelling approach, we explored high resolution data of a single foraging trip. Figure 3 shows an 18 km track on 25 May 2014 from 8.59 to 9.28 UTC (individual 805) as an example. During this segment of a single foraging trip, the bird flew close to the ground along a dike, initially switching between flight modes along part of the dike, then using soaring flight further along the dike. When it left the dike it used all flight modes over land until it found thermals above the city (seen in clear climbing and gliding cycles, reaching altitudes of more than 700 m), and finally, switched to mainly flapping flight over water as it returned to the colony (figure 3a). This short segment shows just how opportunistic and sensitive to local environmental conditions a gull can be in its flight behaviour. The Dutch landscape is relatively flat, with coastal dunes and dikes resulting in some heterogeneity in local topography (figure 3b). We expect that soaring along dikes was facilitated by orographic lift. For exploratory purposes, we calculated orographic lift for this area at 9.00 UTC following $v(\sin \theta) \cos(\alpha - \beta)$ [9], where v = wind speed, θ = slope angle, α = wind direction, β = terrain aspect and using wind data collected from the meteorological station at De Kooy (www.knmi.nl) and a 5 m digital elevation model of The Netherlands (www.ahn.nl). Figure 3c shows the

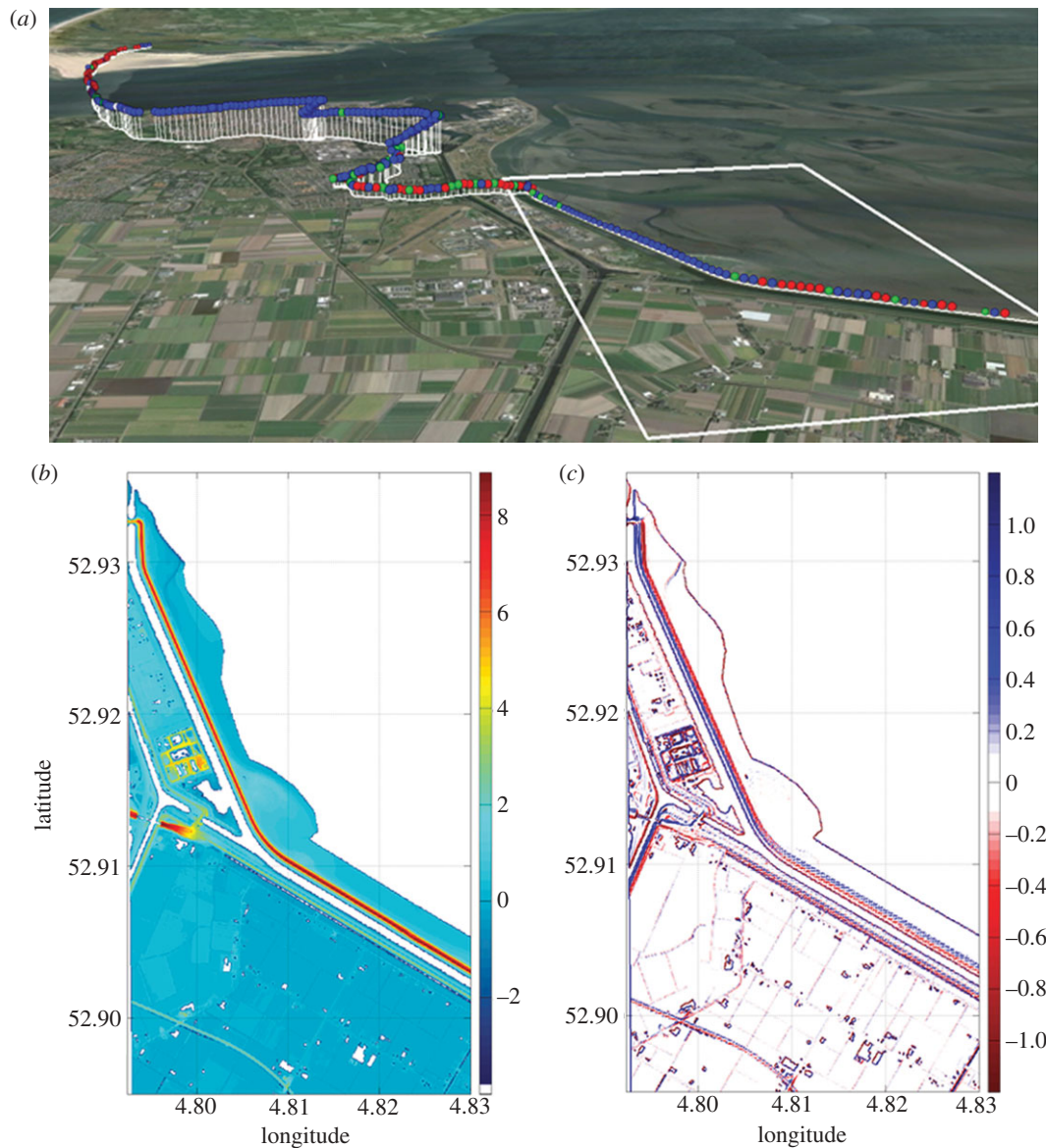


Figure 3. Fine-scale flight behaviour in relation to environmental conditions. (a) High resolution measurements (every 5 s) during part of a foraging trip by individual 805 on 25 May 2014 from 8.59 to 9.28 UTC (red, blue and green indicate flapping, soaring and mixed-flight modes, respectively), (b) 5 m resolution digital elevation model of the area (white areas indicate water), (c) orographic lift (ms^{-1}) at 9.00 UTC, with wind (4.5 ms^{-1}) blowing from the west. The area in (a) shown in subplots (b) and (c) is delineated by a white rectangle.

availability of orographic lift which was higher (orographic lift approx. 1.1 m s^{-1}) along the parts of the dike where the bird used soaring flight compared with the area along the dike where the bird alternated between flapping, soaring and mixed-flight modes (orographic lift approx. 0.6 m s^{-1}).

4. Discussion

Our study shows that lesser black-backed gulls used flapping and soaring flight modes over land and sea, and adjusted their flight behaviour to environmental conditions. As expected, individuals relied predominantly on flapping flight and spent approximately 30% of their time in flight soaring. To provide an estimate of the amount of energy saved by using both flight modes compared with flapping flight alone, we assume that soaring costs $2 \times$ basal metabolic rate (BMR) while flapping flight costs $7 \times$ BMR [30,55]. By soaring 30% of its flight time, a gull would thus reduce its energy expenditure by approximately 21%. In addition to soaring, mixed-flight mode was used to a varying degree between

individuals and is expected to provide additional energetic savings during flight [54,56].

The amount of time spent in flight varied greatly among individuals and increased with the amount of time spent at sea. Individual birds in this colony use a range of foraging strategies from almost completely terrestrial to entirely marine [45]. At sea, birds must search for ephemeral resources over large areas, whereas on land, the location of some terrestrial resources (e.g. waste treatment areas, animal fodder) may be closer to the colony or the locations are more predictable and hence require less flight for searching. Our findings suggest that the energetic investment in flight when foraging at sea is higher than when foraging on land simply due to an increase in the amount of time spent in flight.

As we expected, and similar to findings for several terrestrial bird species [24,53,57,58], the probability of soaring increased with increasing boundary layer height and time of day, reflecting the general diurnal development of the convective boundary layer over land [40]. These are conditions that are especially relevant for thermal soaring, the process of climbing in warm rising and gliding to the next source

of thermal lift. This is a flight mode which is generally attributed to terrestrial birds and only occasionally to seabirds at sea [25,59]. While thermal convection clearly supports soaring flight of lesser black-backed gulls over land, a proportion of the variability in flight mode selection is not explained by our model. Gulls flew predominantly at low flight altitudes (median = 16 m, 95% less than 227 m above surface level) and thus relied on the complex micro-scale spatio-temporal distributions of thermal lift shaped by heterogeneous landscapes [60,61], which are not resolved by medium-range weather models. Low flight altitudes and measured airspeeds during soaring, which were much higher than predicted cross-country airspeeds, also suggest that gulls did not spend extensive amounts of time climbing in thermals. Moreover, soaring flight over land may be powered in different ways, for which local wind speed and direction in relation to the surface roughness and landscape structures are more important than thermal convection.

At sea, the relationship between flight mode and atmospheric conditions may differ from that on land. While thermals may develop at sea under very specific sea–air interactions supporting thermal soaring [25,59], this is probably not the case in the North Sea in early summer. Wind shear may support dynamic soaring close to the water surface as observed in other seabirds [32,42]. In addition to atmospheric conditions that are often measured or modelled, other factors may increase the capacity of birds to use soaring and gliding flight. For example, birds may use aerial turbulence generated by boats to support soaring flight [28,62]. Flying in linear formations also assists in reducing wing beat frequency, increasing gliding propensity and thus reducing the energetic cost of flight [63]. Disentangling the dynamics of the environmental conditions needed to support different forms of soaring flight over land and sea requires further analysis. This is becoming more feasible as higher resolution environmental datasets (e.g. high resolution meteorological models or digital elevation models based on LiDAR) as well as tools to integrate environmental data with movement data are becoming increasingly available [64,65].

Owing to their impact on flight energetics, landscape features and atmospheric conditions will influence foraging costs and may influence foraging strategies, subsequent space use and consequently the time and energy available for self-maintenance and reproduction [66]. Foraging at sea for ephemeral resources may require more time spent in flight, as shown in this study, or more tortuous movement patterns resulting in higher energy expenditure than other foraging strategies [67]. For individuals that use thermal convection for soaring over land, foraging early or late in the day will be more costly than foraging at midday. In species with bi-parental chick care, such as the lesser black-backed gull, this may result in foraging costs that may differ between partners. How birds respond to wind speed and direction will influence the time and energy invested in flight, and may also influence how and where birds forage [29,67–69]. Scaling up beyond the

individual, the aerial environment, due to its impact on flight costs, may influence the distribution of species [70–72]. Thus, flexibility in flight behaviour and the ability to reduce flight costs across a broad range of environmental conditions may facilitate gulls and similarly opportunistic species in adapting to new environments and resources; for example, increasing exploitation of terrestrial landscapes and a dietary shift to terrestrial prey [73,74], increasing use of cityscapes and expansion of their breeding range and breeding habitats.

During flight, birds may select a specific flight mode based on a range of interacting factors whose relative importance depends on external as well as internal drivers [31,75]. These factors may include the motivation to fly (e.g. commute back to colony, bring food to young, search for food, escape or chase conspecifics), individual foraging specializations (e.g. discards, human refuse, terrestrial invertebrates) [45,76] or preferred flight routes. To improve our understanding of the complex relationship between flight behaviour and the environment, we need to study flight behaviour further at a fine scale in the context of individual decision making and trade-offs. Subsequently we can scale-up findings to derive eco-evolutionary informative generalizations across populations and species.

Data accessibility. All raw tracking data are stored in the UvA-BiTS centralized database [38]. The GPS data annotated with behavioural classes and derived meteorological variables are available via Dryad (<http://dx.doi.org/10.5061/dryad.j6s47>). ECMWF meteorological data are available via national contact institutes; for more information see www.ecmwf.int. The World Light Gray Base Map and the ESRI Ocean Mask World 1 km are publicly available via the ESRI ArcGIS online map service.

Authors' contributions. J.S.-B., W.B. and E.E.v.L. conceived the design of the study. C.J.C. contributed to early discussions and led fieldwork in the colony. C.M. developed the framework of behavioural classification. W.B. annotated the accelerometer data and developed the behavioural models. E.E.v.L. developed the framework for modelling soaring probability. W.B. calculated the orographic lift. J.S.-B. designed the tracking measurement schemes and processed the tracking data, coordinated data analysis and interpretation and led all stages of the manuscript writing. All authors have contributed to the content of the article and approved the final version.

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