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An improved method to derive behavioural budgets and energetics from geolocator data in Common Guillemots *Uria aalge*

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Abstract

Light-immersion data from geolocators can be used to estimate behavioural budgets and energetics in seabirds throughout the annual cycle. However, all methods used to categorise time spent in behaviours rely on assumptions that are difficult to validate. Additional data, such as pressure and temperature data from time-depth recorders (TDRs), can help to refine these assumptions. We explore the utility of previous methods to derive behavioural budgets from light-immersion data using a dataset from Common Guillemots *Uria aalge*, where individuals were equipped with both a TDR and a solar Global Location Sensor (GLS), also known as a 'geolocator'. We compared behavioural allocations from previous methods to those derived when also using TDR data. Previous methods used light-immersion data to distinguish between time foraging, active, and resting on the water, but the addition of TDR data revealed that these activities resulted in similar light and immersion levels. It was also more difficult to differentiate between rest and flight using light-immersion data alone. However, by using insights gained from combined light-immersion and TDR data, we developed an improved method to assign behaviours using light-immersion data alone, and provide an adjusted equation to use these data to calculate energetics in Guillemots. We recommend using our approach when processing light-immersion data; however, if detailed activity budgets (particularly foraging information) are required, we recommend using higher resolution loggers, e.g. integrated light-immersion-temperature-pressure devices. Our findings are likely to be relevant for studies of other seabird species (particularly other auks) that dive and spend most of their time at sea during winter.

Introduction

Solar Global Location Sensor (GLS) loggers with immersion sensors ('geolocators') have been widely deployed on seabirds, providing data that can be used to estimate location, activity budgets and energetics throughout the annual cycle. During the breeding season, short-lived higher-resolution loggers can be used to derive seabird locations and behaviour (e.g. Trevail *et al.* 2023; Tremblay *et al.* 2024); however, such loggers often have short battery lives (or batteries that are too large for many species) or fall off when feathers are moulted. Therefore, relatively small and long-lived geolocators have become an important tool for seabird studies conducted outside the breeding period, which have broadened our understanding of seabird ecology (e.g. Militão *et al.* 2022). Geolocators typically record light, saltwater immersion and temperature data, from which location and activity can be derived and subsequently used to estimate energy expenditure (e.g. Pelletier *et al.* 2020). The limitations of using light-immersion data from geolocators to estimate location have been widely discussed (e.g. Halpin *et al.* 2021) yet using these data to allocate time spent in behaviours is less common, thus less attention has been given to validating these methods (although see Dunn *et al.* 2020, Darby *et al.* 2022 and Bennett *et al.* 2024).

A key limitation of using light-immersion data to assign activity budgets is that data are typically stored in a summarised format, for example only the maximum light value across a period (e.g. five or ten minutes), or the proportion of time spent immersed in saltwater across a period (ranging from e.g. five minutes to four hours). It is much more difficult to assign behaviours to these summarised datasets than if the raw data were available, as different behaviours can present with similar immersion patterns. For example, loggers will be dry when birds are in flight or resting on land and wet when birds are submerged in saltwater, but activities with medium immersion levels (such as foraging for surface-feeding seabirds or preening whilst on the water) are difficult to differentiate from those that might include a change of behaviour, such as a take-off from water. In addition, there are a wide variety of geolocator models available, which all record and store data in slightly different ways, meaning that datasets can be difficult to combine or compare.

Most previous studies that use light-immersion data to derive seabird energetics during the non-breeding season have focussed on auks, with a range of methods used to estimate activity budgets (e.g. Fayet *et al.* 2017; Dunn *et al.* 2022). A recent study deployed two devices simultaneously on Common Guillemots (hereafter 'Guillemots') *Uria aalge*, equipping each individual with a time-depth recorder (TDR) on one leg and a geolocator on the other (Buckingham *et al.* 2023). TDRs record pressure data, therefore providing a more accurate estimation of time spent foraging for species such as auks that dive to catch prey than immersion data alone. Additionally, the higher-resolution temperature data recorded by the TDR, and the fact that both legs were equipped with loggers, meant that time spent 'tucking' a leg into plumage (which is typically how auks rest whilst on water; Elliott & Gaston 2014; Linnebjerg *et al.* 2014) could be measured more accurately. This leg-tucking behaviour results in a warm, dry leg and thus can be difficult to differentiate from flight or colony attendance when the tucked leg is equipped with a geolocator, or from foraging or active on the water when the untucked leg is wearing the geolocator (Darby *et al.* 2022). Here, we compare the activity budget derived from both a TDR and geolocator in Buckingham *et al.* (2023) to previous methods of allocating time to behaviours using only light-immersion data. Based on our results, we provide insights into the information that geolocators can provide, develop an improved method for estimating time-activity budgets and energy expenditure for future geolocator-only studies of Guillemots during the non-breeding season, and provide guidance for other similar studies.

Methods

As detailed in full within Buckingham *et al.* (2023), 61 Guillemots from four UK breeding colonies were equipped with both a TDR (Cefas G5 standard) and a geolocator (Lotek MK3006) (Figure 1). Deployments took place during the 2019 breeding season, with loggers retrieved during the 2020 and 2021 breeding seasons. Of the 47 individuals that were re-trapped, four had lost their geolocator and four had devices that failed early in the non-breeding season, so were excluded from analysis (Table 1). Therefore, combined TDR plus geolocator datasets were available from 39 individuals. The combined mass of the two devices plus their colour rings (geolocator: 3.7g; TDR: 4.5g) was 1.07% of the lightest recorded body mass of a breeding Guillemot (765g; Wagner 1999, Harris *et al.* 2000) and therefore consistent with recommendations to minimise additional weight when using tagging devices (Bodey *et al.* 2018, Green *et al.* 2019). We were unable to find any published studies of the device effects from using two leg-mounted loggers, but previous studies have shown no difference in resighting rates, body mass or breeding success between geolocator-tagged auks compared to non-tagged individuals (Fort *et al.* 2012, Baak *et al.* 2021), and one study on Manx Shearwaters *Puffinus puffinus* (which also forage through wing-propelled diving) found no significant difference between individuals deployed with one leg-mounted geolocator and untagged birds with regard to foraging efficiency, trip duration or breeding success (Gillies *et al.* 2020).

Table 1. Sample sizes of deployed and retrieved loggers and processed combined datasets. Four individuals had lost their geolocator upon recapture, and a further four had one or both devices fail early in the non-breeding season, thus were excluded from analyses.

	Retrieved		**Processed**
Deployed	**TDR**	**Geolocator**	**datasets**
61	47	43	39

Figure 1. Photo of time-depth recorder (on the left leg) and geolocation-immersion logger (on the right leg, above the metal BTO ring) on a Common Guillemot *Uria aalge*.

Dual-logger behavioural allocation

Here, we summarise the methods of behavioural allocation using both a TDR and a geolocator (see Buckingham *et al.* 2023 for further details).

Each TDR recorded data for 24 hours every five days, starting on 1 July 2019 until device failure (median fail date 16 March 2020); therefore spanning most of the Guillemot non-breeding season. Pressure and temperature were sampled once every 12 seconds (s). Geolocators recorded data consistently until failure and stored summarised data: light data were sampled once per minute, with the maximum light level stored for each ten-minute bout; saltwater immersion data (wet or dry) were sampled every three seconds and summarised into proportion of time spent immersed for each ten-minute bout; and a temperature was sampled for every 20 minutes that the device was continuously immersed in saltwater. Light-immersion data were processed using the R package probGLS (Merkel *et al.* 2016) to obtain a location for each day, from which astronomical sunset and sunrise times were extracted to infer day (including periods of twilight) and night. TDR data were processed to convert pressure to depth using an R script adapted from Duckworth *et al.* (2020; 2021). The dual-deployed light-immersion and TDR data streams were then linked in time for each individual Guillemot, and used to allocate time to five behaviours (Figure 2), with behaviours allocated in the order stated below:

1. Diving: any time where the pressure logger of the TDR indicated that the individual was submerged below 1 m.
2. Resting on the water's surface: any time that the individual had 'tucked' one leg into its plumage. This was estimated in two ways to reflect the data gathered by each leg's logger. Firstly, time when the TDR was tucked was indicated by the temperature of the TDR being either > 18°C or greater than the geolocator-recorded mean daily sea surface temperature (SST, °C) + 2°C, whichever was higher. Then, after excluding time spent in flight and attending the colony (see below), time when the geolocator was tucked was indicated by low variability of temperatures in the TDR logger (indicating that it was in water, which is more temperature-stable than air, and based on the proportion of fluctuations that were greater than the device sensitivity; Buckingham *et al.* 2023) and the geolocator was between 0-92% wet.
3. Flight: the geolocator was 0% wet and the TDR-recorded temperatures were more variable, indicating that the logger was in air.
4. Colony attendance (a behaviour that Guillemots exhibit throughout the annual cycle at some colonies): any time that the loggers fulfilled the criteria for flight for longer than 30 minutes,

following Dunn *et al.* (2020). For each period of colony attendance, we reallocated the first ten minutes to flight to account for time spent accessing the colony.

5. Active on the water's surface: any remaining time where the geolocator was ≥ 92% wet for that ten-minute bout. This behaviour encompassed rests between dives, swimming, or time preening or interacting with other individuals on the water.

The limit of 92% wet, demarking the difference between active and resting on the water's surface (when the geolocator was tucked), was set to ensure equal time tucking each leg across all processed datasets, under the assumption that individuals may tuck one leg preferentially (Fayet *et al.* 2016) but that this would balance out across individuals. This limit was validated using data collected during the post-breeding moult, when Guillemots moult their flight feathers and so are unable to fly or attend the breeding colony (Birkhead & Taylor 1977, Harris & Wanless 1990). For further details of why these thresholds were chosen, please see Buckingham *et al.* (2023).

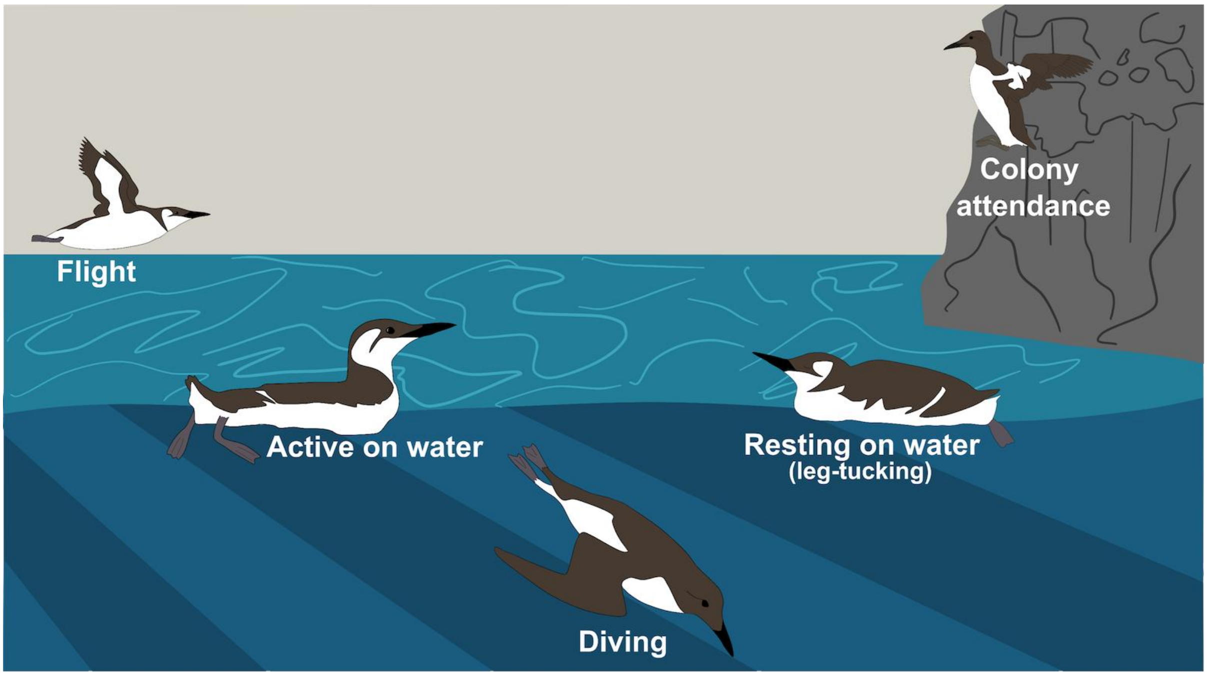

Figure 2. Illustrations of Common Guillemots *Uria aalge* in each behaviour that time was allocated to when using the combined data from time-depth recorders and geolocation-immersion loggers. Individuals are shown in a mix of breeding and non-breeding plumage.

Geolocator-only behavioural allocation

We compared methods for allocating time to foraging following a recent method that used geolocators to estimate activity budgets in Guillemots (Dunn *et al.* 2022). Dunn *et al.* (2022) defined behaviours in the following way:

- Foraging: ≥ 98% wet.
- Flight: ≤ 2% wet for up to two hours during daylight.
- Active on water: between 2 and 98% wet.
- Rest: ≤ 2% wet at night or ≤ 2% wet for more than two hours during the day, encompassing rest on water and land. This value was subsequently adjusted so that a minimum of 42% of each night was spent resting at sea, with time reallocated from active on water as it was assumed that some time active was actually rest time when the non-logger leg was tucked.

We made minor amendments to Dunn *et al.*'s (2022) behavioural allocation process to reflect the differences between the two datasets. We split 'rest' into two sub-categories to aid our subsequent method comparisons: 'rest: day', which could be either time attending the colony or time tucking one leg, and 'rest: night', which was assumed in Dunn *et al.* (2022) to only be time spent tucking one leg. In addition, in the dual-logger method we had time diving, rather than time foraging. These variables are not equivalent, as time foraging also includes pauses between dives. We therefore adjusted the results from the dual-logger method (used in Buckingham *et al.* 2023) by redefining each ten-minute bout with at least one dive as foraging.

Method comparisons

We combined the datasets resulting from each behavioural method and filtered the activity budget created using the geolocator-only data to ensure that we only retained data for days where we had also collected TDR data, as the TDRs only recorded data for one day in every five and we wanted to directly compare the two datasets. We plotted a matrix table to determine how often each ten-minute bout of light-immersion data was being allocated to the same behaviour between the two methods. This analysis was completed on the dataset prior to adjusting the time spent tucking at night, as this required summarising the dataset and so we would not have been able to compare each timestamp individually. However, as we had included 'rest: TDR tucked' in our dual-logger dataset, we could also compare which behaviour this was being allocated to in the geolocator-only approach. We then compared the summarised datasets after adjusting the time spent leg-tucking at night.

Based on our comparison, we then investigated whether we could improve behavioural allocation using light-immersion data only. We tested whether there was a pattern between the immersion data and behaviour as allocated by the dual-logger method by plotting the frequency distribution of percentage time wet during time spent in each of the three behaviours where the geolocator was predominantly wet (foraging, active, and resting with the leg carrying the TDR device tucked i.e. the geolocator leg was likely immersed). We also assessed whether we could use light levels to distinguish between behaviours, as this method has been used previously in a related species (Darby *et al.* 2022). We filtered the dual-logger derived data to be between nautical sunrise and sunset (based on the start time for the ten-minute bout recorded by the geolocator), rescaled light to be between 0 and 100% for each ten-minute bout (i.e. divided it by the maximum possible light level, which was 64 for this logger model), and plotted the percentage light for each ten-minute period within each behaviour. To further investigate this, we filtered the data to the core period when the majority of individuals at our study sites would have been completing their post-breeding moult and so were unable to fly or attend the colony (defined as 16 August to 15 September for our study populations, as in Buckingham *et al.* 2022; 2023) and again plotted the proportion of light for each ten-minute period with each behaviour. Finally, we tested potential maximum flight bout lengths by extracting dry bouts during the period after leaving the breeding colony (as defined in Buckingham *et al.* 2023) and before the first date of colony attendance for the Isle of May (21 October, as defined in Bennett *et al.* 2024).

Behavioural allocation validation

Subsequently, we derived a new method for allocating time to behaviours in auks using only geolocators (detailed in the results). We validated our method by determining the similarity between the activity budgets created using 1) the dual-logger method (Buckingham *et al.* 2023); and 2) the geolocator-only method (as defined above). As with the comparison between Buckingham *et al.* (2023) and Dunn *et al.* (2022), we converted dive time to foraging time within the dual-logger method, combined the resulting datasets and filtered the days to only include days where we had TDR data. We created a matrix table to determine how often each ten-minute bout was allocated to the same behaviour by both methods prior to adjusting for leg-tucking. We then adjusted time spent leg-tucking and compared the summarised datasets.

Energetics adjustment

Within the dual-logger method (Buckingham *et al.* 2023), daily energy expenditure (DEE; kJ) was calculated for each individual using the following equation for a five-behaviour activity budget (Elliott & Gaston 2014; Burke & Montevecchi 2018; Patterson *et al.* 2022):

$$\mathrm{DEE} = 508\ \mathrm{T_{Flight}} + 33\ \mathrm{T_{Colony}} + 3.64 \sum \left[1 - \mathrm{e}^{\frac{-\mathrm{T_{Dive}}}{1.23}}\right] + (113 - 2.75\ \mathrm{SST})\mathrm{T_{Active}} + (72.2 - 2.75\ \mathrm{SST})\mathrm{T_{Rest}}$$

where time resting (T_{Rest}), active (T_{Active}), flying (T_{Flight}) and attending the colony (T_{Colony}) were measured in hours, time diving (T_{Dive}) was the length of each dive in minutes, and SST was the daily mean saltwater temperature (°C) recorded by the geolocator.

Based on our adjustments to the activity budget and resulting behaviours using light-immersion data only, we adjusted the above equation to ensure that DEE was as similar as possible between the dual-logger and geolocator-only methods by combining behaviours and adjusting the coefficients accordingly.

Results

Method comparisons

Overall, over twice as much time was allocated to time foraging using the geolocator-only method (Dunn *et al.* 2022) compared to the dual-logger method (Buckingham *et al.* 2023; Table 2), with around 60% of foraging events from the geolocator-only method allocated to time active or resting with the TDR tucked using the dual-logger method (Table 3). Additionally, much more time was allocated to active on the water and resting and much less to flight using the dual-logger method compared to the geolocator only method, even after Dunn *et al.*'s (2022) night-time leg-tucking adjustment (Table 2). Overall, we observed no clear immersion threshold (i.e. percentage wetness) delimiting time foraging, active or resting with the TDR tucked (Figure 3).

We observed very little variation in light levels across the three behaviours where the geolocator was wet (i.e. foraging, active, and resting with the TDR tucked; Figure S1). We observed slightly more variation within the dry behaviours (i.e. resting with the geolocator tucked, flight, and colony attendance), but during the post-breeding moult (as defined in the methods), when we only observed four behaviours when using the dual-logger method (i.e. there was no flight or colony attendance), there was very little variation in light level across the behaviours, with all showing high levels of light exposure (Figure S2).

Most dry bouts during the period after leaving the breeding colony and before the first date of colony attendance for the Isle of May (see methods) were ten minutes long, but ranged up to a maximum of 30 minutes across all populations (Figure S3).

Table 2. Summarised total hours across all processed datasets using the dual-logger method (Buckingham *et al.* 2023) and the geolocator only method from Dunn *et al.* (2022), both prior to and after the night-time leg-tucking adjustment.

	Hours		
Behaviour	**Buckingham**	**Dunn (pre-adjustment)**	**Dunn (post adjustment)**
Foraging	4,516	10,421	10,421
Active	5,062	2,605	1,230
Rest	3,702	221	556
Flight	16	49	49

Table 3. Matrix of behaviours allocated to each ten-minute bout of immersion data using the dual-logger method (Buckingham *et al.* 2023) and the geolocator only method (Dunn *et al.* 2022), prior to further adjustments (which are only relevant for summarised data). Each value represents one ten-minute bout of immersion data, and is plotted according to the behaviour it was categorised into using each method; percentages are the values allocated to each behaviour compared to the total number of bouts across all processed datasets. Green shading indicates the equivalent behaviours between the methods, i.e. the behaviours we would expect the same bout of immersion to be grouped into based on each method.

		Geolocator only (Dunn *et al.* 2022)					
	Behaviour	**Foraging**	**Active**	**Rest: night**	**Rest: day**	**Flight**	
Dual-logger (Buckingham *et al.* 2023)	**Foraging**	70,831 (26.71%)	16,703 (6.30%)	131 (0.05%)	75 (0.03%)	211 (0.08%)	**87,951 (33.17%)**
	Active	66,364 (25.03%)	13,497 (5.09%)	0	0	0	**79,861 (30.12%)**
	Rest: TDR tucked	40,200 (15.16%)	1,647 (0.62%)	36 (0.01%)	220 (0.08%)	31 (0.01%)	**42,134 (15.89%)**
	Rest: geolocator tucked	0	43,481 (16.40%)	7,572 (2.86%)	1,003 (0.38%)	1,999 (0.75%)	**54,055 (20.38%)**

Rest: colony	0	0	331 (0.12%)	269 (0.10%)	86 (0.03%)	**686 (0.26%)**
Flight	0	39 (0.01%)	184 (0.07%)	42 (0.02%)	227 (0.09%)	**492 (0.19%)**
	177,395 (66.90%)	**75,367 (28.42%)**	**8,254 (3.11%)**	**1,609 (0.61%)**	**2,554 (0.96%)**	**265,179 (100%)**

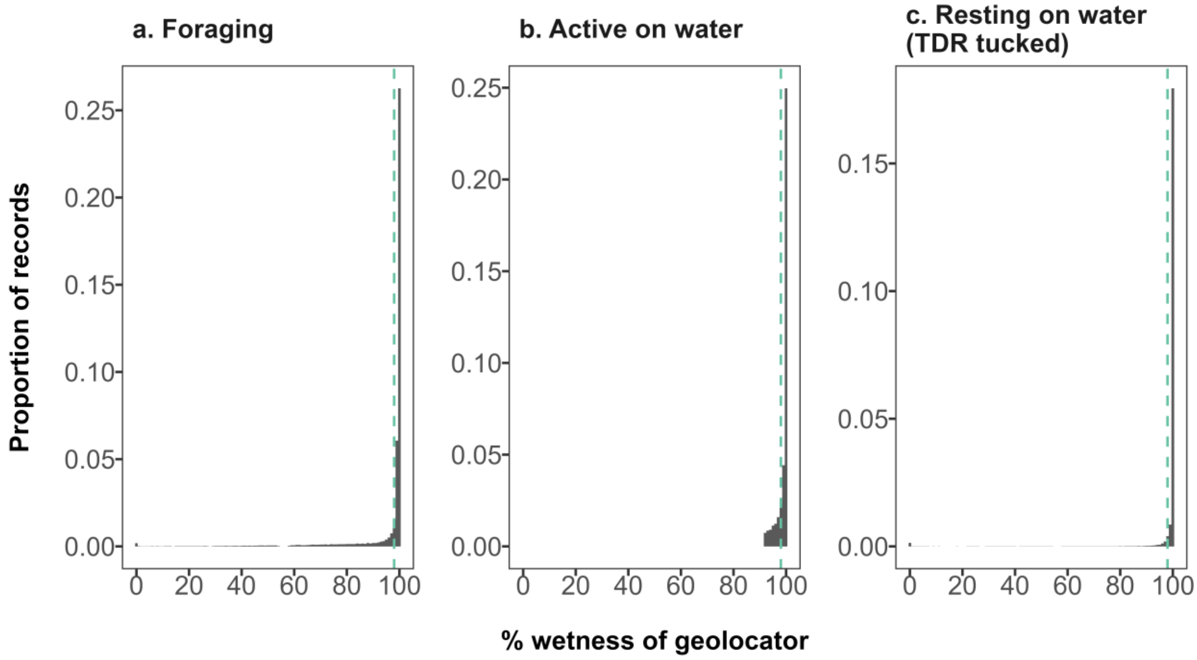

Figure 3. Histogram of percentage wetness of the geolocator device during three activities (diving; active on water; or resting on water with the time-depth recorder **(**TDR) device tucked), where behaviours were allocated using dual-deployed TDR and light-immersion data (Buckingham *et al.* 2023). Bars indicate the proportion of total records for each immersion percentage. The dashed green line indicates 98% wet, the threshold used to define foraging in Dunn *et al.* (2022).

Adjusted method to allocate behaviours using light-immersion data

As we could not reliably differentiate 'foraging' and 'active on water' behaviours, we combined these behaviours into one behavioural classification 'foraging or active' with a subsequent adjustment (see below) to account for some of this time being time resting with the non-geolocator leg tucked. We therefore defined a budget consisting of four behaviours: foraging or active on water, resting on water (tucking either leg), flight, and colony attendance (resting on land). A flow diagram summarises this procedure (Figure 4).

We allocated timings of day (including twilight) and night based on location (see 'Dual-logger behavioural allocation' and as in Dunn *et al.* 2020; 2022). When the geolocator was dry (0% wet) during daylight hours, we allocated time to flight if the geolocator was dry for 30 minutes or less (i.e. three successive ten-minute bouts that were 100% dry), or resting at the colony if it was dry for more than 30 minutes, in line with Dunn *et al.* (2020) and our observations during the period of assumed no colony attendance (Figure S3). Dunn *et al.* (2020) and Bennett *et al.* (2024) assumed that no flight or colony attendance behaviours occurred during the night, which was appropriate for individuals from the colony that was the focus of those studies (the Isle of May) given local observations (Harris & Wanless 2016; Bennett *et al.* 2024). However, there is evidence for night-time colony attendance occurring at one Guillemot colony in close proximity to the colonies within this study (Sumburgh Head, Shetland; Sinclair *et al.* 2017). As there is no evidence for Guillemots flying or arriving at the colony during the night, we did not allow flight during night and therefore only allowed colony attendance during the night if the geolocator was dry for the entire night, in which case we assigned colony attendance to the full night-time period. All other dry spells during the night were allocated to resting on water (see below).

As in previous methods, we defined resting on water as time when one leg was tucked into the plumage. We only had information from one leg, so we assigned this behaviour in two stages. We initially defined records where the geolocator was 0% wet during the night (but not classed as colony attendance) or between 0-92% wet at any time as resting on water, the value set to equalise time spent tucking legs within the dual-logger method (Buckingham *et al.* 2023). Time foraging or active on water was therefore initially defined as records where the geolocator was 92% wet or more, representing time when individuals were diving, pausing between dives, swimming, preening or socialising on the water. Then, as individuals are likely to spend limited periods of time tucking both legs (Fayet *et al.* 2016; Darby *et al.* 2022), we calculated the difference between time resting on water with the geolocator tucked and with the TDR tucked. We multiplied our initial value of time resting on water by this correction factor (1.8) to equalise time spent leg-tucking between the legs across all processed datasets. This gave a final value for resting on water, with time reassigned from our initial value of time foraging or active on water. Where there was insufficient time foraging or active on water to reassign to fulfil this criterion, we reassigned all available time of foraging or active on water to resting on water.

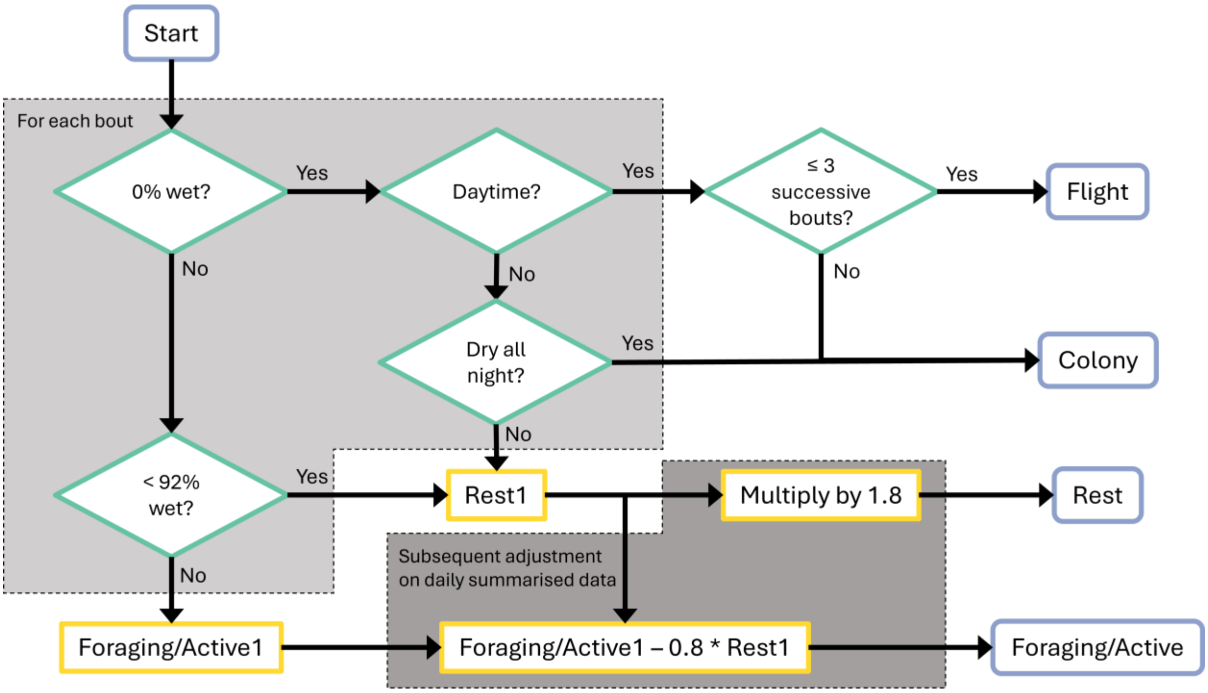

Figure 4. Diagram of adjusted behavioural classification method using light-immersion data only. Processes that apply to each individual ten-minute bout of immersion data are in the light grey box. Processes that apply to daily summarised data (after behaviours Rest1 and Foraging/Active1 have been defined) are in the dark grey box).

Behavioural allocation validation

As expected, as we had set the threshold values using the dual-logger method and applied this to the geolocator-only method, the total number of ten-minute immersion bouts allocated to foraging/active using the geolocator-only method (197,035) was similar to but slightly lower than bouts allocated to foraging, active and resting on water with the TDR tucked from the dual-logger method (209,954; Table 4). Using the geolocator-only method, some foraging events (from the dual-logger method) were classified as resting with geolocator tucked in the geolocator-only method (Table 4), likely due to a change in behaviour occurring within the ten-minute bout, e.g. both a dive and a flight or leg-tuck. As the dual-logger method classified diving events as its first step, and we then converted any ten-minute bout with a dive into ‘foraging’, it is difficult to say how we could improve on that using the relatively low-resolution immersion data available when using only a geolocator. However, our additional steps to equalise time leg-tucking resulted in foraging/active and rest time being relatively similar overall between the two methods across all processed datasets (Table 5).

Table 4. Matrix of behaviours allocated to each ten-minute bout of immersion data using the dual-logger method (Buckingham *et al*. 2023) and the geolocator only method developed in this study, prior to further adjustments (which are only relevant for summarised data). Each value represents one ten-minute bout of immersion data, and is plotted according to the behaviour it was categorised into using each method; percentages are the values allocated to each behaviour compared to the total number of bouts across all processed datasets. Green shading indicates the equivalent behaviours between the methods, i.e. the behaviours we would expect the same bout of immersion to be grouped into based on each method.

		Geolocator only (this study)				
	Behaviour	**Foraging /active**	**Rest: geolocator tucked**	**Rest: colony**	**Flight**	
Dual-logger (Buckingham *et al.* 2023)	**Foraging**	75,929 (28.63%)	11,767 (4.44%)	125 (0.05%)	138 (0.05%)	**87,959 (33.17%)**
	Active	79,861 (30.11%)	0	0	0	**79,861 (30.11%)**
	Rest: TDR tucked	41,244 (15.55%)	641 (0.24%)	238 (0.09%)	11 (0.00%)	**42,134 (15.89%)**
	Rest: geolocator tucked	0	51,403 (19.38%)	1,716 (0.65%)	936 (0.35%)	**54,055 (20.38%)**
	Rest: colony	0	331 (0.12%)	333 (0.13%)	22 (0.01%)	**686 (0.26%)**
	Flight	1 (0.00%)	222 (0.08%)	54 (0.02%)	215 (0.08%)	**492 (0.19%)**
		197,035 (74.30%)	**64,364 (24.27%)**	**2,466 (0.93%)**	**1,322 (0.50%)**	**265,187 (100%)**

Energetic adjustment

As we grouped foraging and active on water when using geolocator-only data, we were required to also group these behaviours within our energy expenditure calculations. We used the dual-logger dataset (Buckingham *et al.* 2023) to derive a new constant for foraging/active that resulted in similar values of energy expenditure when these behaviours were derived using light-immersion data only compared to the dual-logger method. Firstly, we summed the daily energy expenditure across all dives by each individual using the dual-logger dataset (with energy expenditure during diving calculated using equation 1). We then calculated an hourly rate of energy expenditure whilst diving (R_{Dive}) by dividing the energy expenditure during diving by the total number of hours spent diving for each individual each day (T_{Dive}). Mean R_{Dive} across all individuals and days in our dataset was 105 kJ h^{-1}. Subsequently, we calculated a new energetic rate for the combined behaviour of foraging/active using the following equation:

$$\mathrm{R}_{\mathrm{Foraging/Active}} = \frac{\mathrm{T}_{\mathrm{Dive}} * \mathrm{R}_{\mathrm{Dive}} + \mathrm{T}_{\mathrm{Active}} * (113 - 2.75 * \mathrm{SST})}{(\mathrm{T}_{\mathrm{Dive}} + \mathrm{T}_{\mathrm{Active}})} + 2.75 * \mathrm{SST}$$

where T_{Dive} and T_{Active} were the hours diving and active, respectively, R_{Dive} was the rate of energy expenditure during diving as calculated above, and SST was the mean saltwater temperature (°C) recorded by the geolocator. All values were measured per individual per day. Mean $R_{ForagingActive}$ at 0°C across all individuals and days was 117.9 kJ h^{-1}.

We then calculated the SST threshold that delimits the temperature below which Guillemots expend additional energy on thermoregulation for each behaviour where SST was a factor. Deriving this threshold was necessary as higher temperatures cannot reduce metabolic rates below the resting or baseline rates in endotherms. We used the constant from T_{Colony} (33 kJ h^{-1}) as our metabolic rate at rest. We determined the temperature thresholds by calculating when the rates of energy expenditure during T_{Colony} and $T_{Foraging/Active}$ fell below the resting rate. For example, the rate of energy expenditure for T_{Rest} was calculated as:

$$(72.2 - 2.75 * \mathrm{SST}) * \mathrm{T}_{\mathrm{Rest}}$$

We rearranged this equation to find the value of SST at which this rate fell below 33 and did the same for $T_{Foraging/Active}$. For T_{Rest}, this temperature was 14.18°C and for $T_{Foraging/Active}$, this value was 30.9°C. Thus, Guillemots need to expend additional energy on thermoregulation when SST is below these values for each respective behaviour.

Within our dataset, SST was always below 30.9°C, thus we always incorporated SST when estimating energy expenditure during foraging/active. We incorporated SST during rest when temperature values were below 14.18°C only. When SST was above 14.18°C during resting on water, we assigned the same energetic cost to this behaviour as we had to time resting at the colony.

This process resulted in two equations for calculating DEE (kJ) in Guillemots using behaviours derived using the geolocator-only method:

1) When the daily mean SST < 14.18°C

$$\mathrm{DEE} = 508\ \mathrm{T_{Flight}} + (118 - 2.75 * \mathrm{SST})\mathrm{T_{Foraging/Active}} + 33\ \mathrm{T_{Colony}} + (72 - 2.75 * \mathrm{SST})\mathrm{T_{Rest}}$$

2) When the daily mean SST ≥ 14.18°C

$$\mathrm{DEE} = 508\ \mathrm{T_{Flight}}\ + (118 - 2.75 * \mathrm{SST})\mathrm{T_{Foraging/Active}} + 33(\mathrm{T_{Colony}} + \mathrm{T_{Rest}})$$

using the number of hours spent in each of foraging/active, rest, flight and colony attendance, and where SST was the mean saltwater temperature (°C) recorded by the geolocator.

Energetics validation

We tested the similarity in energy expenditure between the two methods. We summed energy expenditure during both time diving and time active on the water per individual per day for the dual-logger method and compared this to energy expenditure during time foraging or active using the geolocator-only method.

Energy expenditure during foraging/active and resting on the water were reasonably similar between the two methods (Table 5). As discussed above, the geolocator-only method estimated more time spent in flight and attending the colony than the dual-logger method, resulting in greater energy expenditure in these behaviours (Table 5) and slightly higher DEE overall (Table 5; Figure 5).

Table 5. Summed hours across all processed datasets in each behaviour and energy expenditure for each behavioural allocation method. This summary was calculated after the leg-tucking correction for the geolocator-only dataset.

	Hours		**Energy expenditure (kJ)**	
Behaviour	**Dual-logger**	**Geolocator-only**	**Dual-logger**	**Geolocator-only**
Foraging/Active	24,864	24,398	2,125,040	2,088,533
Rest	18,838	19,101	748,330	760,900
Flight	102	219	51,926	111,167
Colony	115	394	3,789	13,008
Total	**43,918**	**44,112**	**2,929,085**	**2,973,609**

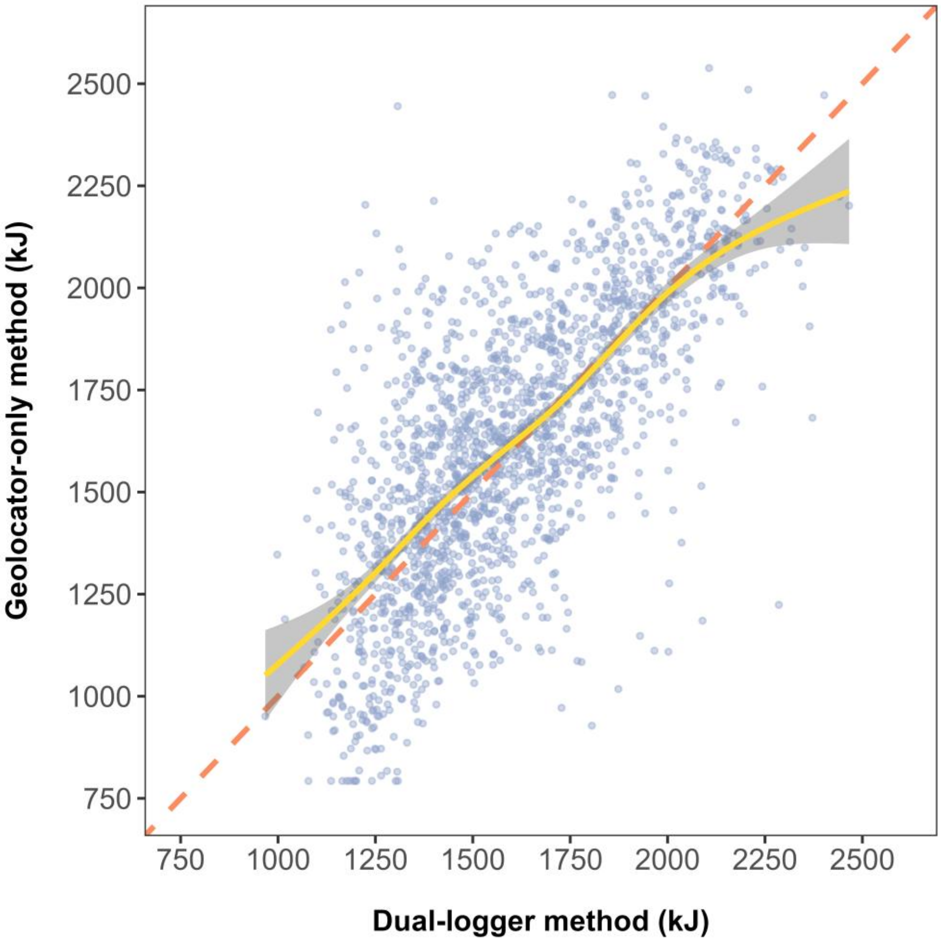

Figure 5. A comparison of overall DEE calculated using each behavioural method approach. Each data point is an individual on a given day, with its position on the x-axis indicating how much energy it expended when behaviours and energetics were allocated using the dual-logger method, and its position on the y-axis when allocated through the geolocator-only method. The solid yellow line represents the smooth for each method of behavioural allocation, with the grey bar representing the

area within the 95% confidence intervals. The orange dashed line represents an equal slope between x and y, i.e. if energetics were perfectly aligned between the methods, the blue points and yellow line would line up against this exactly.

Discussion

Many previous efforts to classify seabird behaviour from light-immersion data were based on assumptions that could not be validated at that time. Overall, the steps we have described above have resulted in an activity budget and energy expenditure (Table 5; Figure 5) using light-immersion data that is reasonably comparable to the activity budget and energy expenditure calculated when these data were combined with TDR data. However, we have highlighted several limitations that should be noted when using only light-immersion data to estimate time budgets and energy expenditure.

Most importantly, we were unable to extract foraging behaviour from light-immersion data, meaning geolocators are not an appropriate method for identifying key foraging times or locations for diving species of seabird that spend a lot of time on the water, such as auks. Therefore, if detailed information on foraging behaviour is required, we recommend deploying loggers that collect higher resolution temperature and pressure data as well as light-immersion data.

Distinguishing between when an individual was truly dry (i.e. in flight or resting on land) versus resting at sea (tucking one leg) was easier with the addition of the TDR device. The dual-logger method provided us with data from each leg, enabling leg-tucking to be classified more accurately than when only one leg was tagged. Leg-tucking was more easily identifiable when the TDR-equipped leg was tucked, as the temperatures were much higher than those recorded by the geolocator, yet the geolocator was immersed, indicating that the individual was not out of the water in high air temperatures. Similarly, tucking of the geolocator-equipped leg was easier to identify when combined with TDR data, as the TDR temperature data were more stable when immersed in water, indicating that only one of the legs was dry. Leg-tucking will always be difficult to accurately measure when only one leg is deployed with a logger, but use of the correction factor described in this study, based on data collected from both legs of multiple individuals, will improve estimations of leg-tucking for studies where only one leg is tagged.

Differentiating between flight and colony attendance was difficult when using either method, and relied on a time limit for flight to allocate the behaviours, as in previous studies (Dunn *et al.* 2020; 2022; Buckingham *et al.* 2023; Bennett *et al.* 2024). We did not to include distance from the breeding colony to determine whether colony attendance was possible, as many individuals within our study remained near the breeding colonies for much of the non-breeding season (Buckingham *et al.* 2023) and due to the low spatial resolution of geolocator data (Halpin *et al.* 2021); however, this measure may be more relevant for studies where individuals range more widely. Using the geolocator-only method, two individuals (which both bred at Whinnyfold) had a single night (17 March 2020) that was dry for its entirety and so reassigned from resting with the geolocator tucked to colony attendance. We had expected this to be a relatively rare behaviour, so it was reassuring that we observed few occurrences of this behaviour. In addition, this result matched with camera observations of no night-time colony attendance for Guillemots on the Isle of May (Bennett *et al.* 2024). If logistically possible, local validation of colony attendance during the non-breeding season could help determine where nighttime colony attendance is likely, and how frequently colony attendance occurs across populations, as this behaviour appears to be more common in the UK compared to e.g. northwest Atlantic populations (Runnels *et al.* 2024).

We allowed a slightly longer maximum period of flight-time (30 minutes rather than 20) than used by Bennett *et al.* (2024), based on our analyses of dry bout lengths during the period between Guillemots leaving the breeding colony and returning later in the autumn (Figure S3). It is therefore possible that flight times may be colony-specific, as the individuals within our study and Bennett *et al.*'s (2024) remained closer to the breeding site throughout the non-breeding season than those breeding in e.g., mid-Norway (Lorentsen & May 2012); however, auks can complete significant migrations whilst flightless, by swimming and using local currents (Merkel *et al.* 2023). We therefore advise taking validation steps, such as the ones taken within this study, to test the possible lengths of flights for other populations. When using the geolocator-only method, estimates of time in flight and attending the colony were higher than when using the dual-logger method, with most of these additional records classed as resting with the geolocator tucked using the dual-logger dataset (Table 2). All of these behaviours (flight, colony attendance, and tucking the geolocator) involve a dry or mostly dry geolocator, but additional information on TDR temperature stability (an indicator of whether the TDR was wet or dry) was not available for the geolocator-only method. As time spent attending the colony and resting on the water have similar energetic costs, the energetic consequences of misidentifying time resting on water as time attending the colony are relatively small. However, the energetic consequences of misidentifying time resting as time in flight are greater, as flight is a very energetically costly activity for auks (Schraft *et al.* 2019). To counteract this, and because there was higher uncertainty when distinguishing between these behaviours than when using the dual-logger method, we did not allocate the first ten minutes of time spent attending the colony to time in flight, as we had done with the dual-logger method.

We adapted Elliott *et al.*'s (2013, as corrected in Patterson *et al.* 2022) formula to estimate non-breeding season energy expenditure in Guillemots. Although this formula was originally derived based on data from a relatively small sample of Brünnich's Guillemots *Uria lomvi*, and made several assumptions (e.g., leg tucks were assumed to be time spent resting on the water, a breeding season body mass was used, yet mass is likely to vary throughout the annual cycle, and the cost of moulting and replacing feathers was not incorporated; Elliott & Gaston 2014), it has been widely applied to calculate energy expenditure in both Brünnich's and Common Guillemots (e.g., Burke & Montevecchi 2018; Dunn *et al.* 2020, 2022, 2023; Patterson *et al.* 2022; Buckingham *et al.* 2023; Bennett *et al.* 2024), and adapted for use in other species of auk (Fayet *et al.* 2016; Dunn *et al.* 2023).

We did not incorporate light measured directly by the logger in our behavioural allocation process, in contrast to Darby *et al.* (2022) and Bennett *et al.* (2024), based on our observation of low variation in light exposure across each behaviour (Figures S1 & S2). Our light data were summarised at a lower resolution to those used in Darby *et al.* (2022), where loggers recorded the maximum light within each five-minute period, compared to our ten-minute periods; thus if the leg was exposed to light for one of the readings during a ten-minute period, the bout was recorded as fully light even if it had been tucked for the majority of the time. However, both Darby *et al.* (2022) and Bennett *et al.* (2024) focussed on extracting specific aspects of auk behaviour (moult and colony attendance, respectively), whereas our main aim was to derive a full behavioural algorithm for Guillemots during the non-breeding season. As the level of shading experienced at the breeding colony varies significantly among Guillemot colonies, the inclusion of light to define colony attendance may not be applicable across many study populations. Finally, during the post-breeding moult, the geolocator-only method allocated only 0.30% and 0.23% of time to flight and colony attendance, respectively. It is likely that at this point of the annual cycle, these records were in fact leg-tucking behaviours, but we believe that this is a minimal margin of error given the resolution of our data.

Overall, if detailed information on foraging activity or colony attendance is required, or highly accurate estimations of energy expenditure are needed, we recommend loggers with a range of sensors. However, for legacy datasets, smaller species that are unable to carry higher-resolution loggers, or studies with budgetary constraints, our approach provides a robust way to estimate behaviour and energetics in Guillemots. Our method could also be adapted for other species of auks, by adjusting the maximum length of each flight bout, the inclusion of colony attendance as a possible behaviour, and allometrically scaling the constants used to calculate the energetic cost of each activity (as in Fayet *et al.* 2016 and Dunn *et al.* 2023). Assigning behaviour from biologging only data is challenging, and 100% accuracy is an unreasonable expectation (e.g. Bennison *et al.* 2018; Patterson *et al.* 2019), but any imprecision using this method will likely be similar between individuals, colonies and over time, making this approach appropriate for comparative research questions (e.g. Fayet *et al.* 2017).

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References

Baak, J. E., Leonard, M. L., Gjerdrum, C., Dodds, M. D. & Ronconi, R. A. 2021. Non-breeding movements and foraging ecology of the Black Guillemot *Cepphus grylle* in Atlantic Canada. *Marine Ornithology* 49: 57-70.

Bennett, S., Daunt, F., Searle, K. R., Harris, M. P., Buckingham, L., Duckworth, J., Dunn, R. E., Wanless, S., Newell, M. A. & Green, J. A. 2024. Distribution and time budgets limit occupancy of breeding sites in the nonbreeding season in a colonial seabird. *Animal Behaviour* 216: 213-233. https://doi.org/10.1016/j.anbehav.2024.07.023

Bennison, A., Bearhop, S., Bodey, T. W., Votier, S.C., Grecian, W. J., Wakefield, E. D., Hamer, K. C. & Jessopp, M. 2018. Search and foraging behaviors from movement data: A comparison of methods. *Ecology and Evolution* 8: 13-24. https://doi.org/10.1002/ece3.3593

Birkhead, T. R. & Taylor, A. M. 1977. Moult of the guillemot *Uria aalge. Ibis* 119(1): 80-85. https://doi.org/10.1111/j.1474-919X.1977.tb02048.x

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C. & Bearhop, S. 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods in Ecology and Evolution* 9: 946-955. https://doi.org/10.1111/2041-210X.12934

Buckingham, L., Daunt, F., Bogdanova, M. I., Furness, R. W., Bennett, S., Duckworth, J., Dunn, R. E., Wanless, S., Harris, M. P., Jardine, D. C., Newell, M. A., Ward, R. M., Weston, E. D. & Green, J. A. 2023. Energetic synchrony throughout the non-breeding season in common guillemots from four colonies. *Journal of Avian Biology* 2023: 1-2. https://doi.org/10.1111/jav.03018

Burke, C. M. & Montevecchi, W. A. 2018. Taking the Bite Out of Winter: Common Murres (Uria aalge) Push Their Dive Limits to Surmount Energy Constraints. *Frontiers in Marine Science* 5: e00063. https://doi.org/10.3389/fmars.2018.00063

Darby, J. H., Harris, M. P., Wanless, S., Quinn, J. L., Bråthen, V. S., Fayet, A. L., Clairbaux, M., Hart, T., Guilford, T., Freeman, R. & Jessopp, M. J. 2022. A new biologging approach reveals unique flightless molt strategies of Atlantic puffins. *Ecology and Evolution* 12(12): e9579. https://doi.org/10.1002/ece3.9579

Duckworth, J., O'Brien, S., Petersen, I. K., Petersen, A., Benediktsson, G., Johnson, L., Lehikoinen, P., Okill, D., Väisänen, R., Williams, J., Williams, S., Daunt, F. & Green, J. A. 2021. Spatial and temporal variation in foraging of breeding red-throated divers. *Journal of Avian Biology* 52: e02702. https://doi.org/10.1111/jav.02702

Duckworth, J., O'Brien, S., Väisänen, R., Lehikoinen, P., Petersen, K., Daunt, F. & Green, J. 2020. First biologging record of a foraging red-throated loon *Gavia stellata* shows shallow and efficient diving in freshwater environments. *Marine Ornithology* 48: 17-22. https://doi.org/10.5038/2074-1235.48.1.1341

Dunn, R. E., Green, J. A., Wanless, S., Harris, M. P., Newell, M. A., Bogdanova, M. I., Horswill, C., Daunt, F. & Matthiopoulos, J. 2022. Modelling and mapping how common guillemots balance their energy budgets over a full annual cycle. *Functional Ecology* 36: 1612-1626. https://doi.org/10.1111/1365-2435.14059

Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P. & Green, J. A. 2020. A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Scientific Reports* 10: 5993. https://doi.org/10.1038/s41598-020-62842-x

Dunn, R. E., Duckworth, J. & Green, J. A. 2023. A framework to unlock marine bird energetics. *Journal of Experimental Biology* 226: jeb246754. https://doi.org/10.1242/jeb.246754

Elliott, K. H. & Gaston, A. J. 2014. Dive behaviour and daily energy expenditure in Thick-billed Murres *Uria lomvia* after leaving the breeding colony. *Marine Ornithology* 42: 183-189. https://doi.org/10.5038/2074-1235.42.2.1088

Fayet, A. L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K. E., Fifield, D., Fitzsimmons, M. G., Hansen, E. S., Harris, M. P., Jessopp, M., Kouwenberg, A-L., Kress, S., Mowat, S., Perrins, C. M., Petersen, A., Petersen, I. K., Reiertsen, T. K., Robertson, G.J., Shannon, P., Sigurðsson, I. A., Shoji, A., Wanless, S. & Guilford, T. 2017. Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird. *Current Biology* 27: 3871-3878. https://doi.org/10.1016/j.cub.2017.11.009

Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H. L., Dean, B. J., Perrins, C. M. & Guilford, T. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behavioral Ecology* 27: 1061-1072. https://doi.org/10.1093/beheco/arw013

Fort, J., Beaugrand, G., Grémillet, D. & Phillips, R. A. 2012. Biologging, remotely-sensed oceanography and the continuous plankton recorder reveal the environmental determinants of a seabird wintering hotspot*. PLoS One* 7: e41194. https://doi.org/10.1371/journal.pone.0041194

Geen, G. R., Robinson, R. A. & Baillie, S. R. 2019. Effects of tracking devices on individual birds - a review of the evidence. *Journal of Avian Biology* 50: e01823. https://doi.org/10.1111/jav.01823

Gillies, N., Fayet, A. L., Padget, O., Syposz, M., Wynn, J., Bond, S., Evry, J., Kirk, H., Shoji, A., Dean, B., Freeman, R. & Guilford, T. 2020. Short-term behavioural impact contrasts with long-term fitness consequences of biologging in a long-lived seabird. *Scientific Reports* 10: 15056. https://doi.org/10.1038/s41598-020-72199-w

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z. & Cruz-Flores, M. 2021. Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods in Ecology and Evolution* 12(11): 2243-2255. https://doi.org/10.1111/2041-210X.13698

Harris, M. P. & Wanless, S. 1990. Moult and autumn colony attendance of auks. *British Birds* 83: 55-66.

Harris, M. P., Wanless, S. & Webb, A. 2000. Changes in body mass of Common Guillemots *Uria aalge* in southeast Scotland throughout the year: Implications for the release of cleaned birds. *Ringing & Migration* 20: 134-142. https://doi.org/10.1080/03078698.2000.9674235

Harris, M. P. & Wanless, S. 2016. The use of webcams to monitor the prolonged autumn attendance of Guillemots on the Isle of May in 2015. *Scottish Birds* 36(1): 3-9.

Linnebjerg, J. F., Huffeldt, N. P., Falk, K., Merkel, F. R., Mosbech, A. & Frederiksen, M. 2014. Inferring seabird activity budgets from leg-mounted time-depth recorders. *Journal of Ornithology* 155: 301-306. https://doi.org/10.1007/s10336-013-1015-7

Lorentsen, S-H. & May, R. 2012. Inter-breeding movements of common guillemots (*Uria aalge*) suggest the Barents Sea is an important autumn staging and wintering area. *Polar Biology* 35: 1713-1719. https://doi.org/10.1007/s00300-012-1215-2

Merkel, B., Phillips, R. A., Descamps, S., Yoccoz, N. G., Moe, B. & Strøm, H. 2016. A probabilistic algorithm to process geolocation data. *Movement Ecology* 4(1): 26. https://doi.org/10.1186/s40462-016-0091-8

Merkel, B., & Strøm, H. 2023. Post-colony swimming migration in the genus Uria. *Journal of Avian Biology* 2024(1-2): e03153. https://doi.org/10.1111/jav.03153

Militão, T., Sanz-Aguilar, A., Rotger, A. & Ramos, R. 2022. Non-breeding distribution and at-sea activity patterns of the smallest European seabird, the European Storm Petrel (*Hydrobates pelagicus*). *Ibis* 164(4): 1160-1179. https://doi.org/10.1111/ibi.13068

Patterson, A., Gilchrist, H. G., Chivers, L., Hatch, S. & Elliott, K. 2019. A comparison of techniques for classifying behavior from accelerometers for two species of seabird. *Ecology and Evolution* 9: 3030-3045. https://doi.org/10.1002/ece3.4740

Patterson, A., Gilchrist, H. G., Robertson, G. J., Hedd, A., Fifield, D. A. & Elliott, K. H. 2022. Behavioural flexibility in an Arctic seabird using two distinct marine habitats to survive the energetic constraints of winter. *Movement Ecology* 10: 45. https://doi.org/10.1186/s40462-022-00344-3

Pelletier, D., Seyer, Y., Garthe, S., Bonnefoi, S., Phillips, R. A. & Guillemette, M. 2020. So far, so good… Similar fitness consequences and overall energetic costs for short and long-distance migrants in a seabird. *PLoS ONE* 15(3): e0230262. https://doi.org/10.1371/journal.pone.0230262

Runnells, E. S., Montevecchi, W. A. & Davoren, G. K. 2024. Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murres during the non-breeding season in the Northwest Atlantic. *Marine Ecology Progress Series* 739: 241-256. https://doi.org/10.3354/meps14614

Schraft, H. A., Whelan, S. & Elliott, K. H., 2019. Huffin' and puffin: seabirds use large bills to dissipate heat from energetically demanding flight. *Journal of Experimental Biology* 222(21): 212563. https://doi.org/10.1242/jeb.212563

Sinclair, N. C., Harris, M. P., Nager, R. G., Leakey, C. D. B. & Robbins, A. M. C. 2017. Nocturnal colony attendance by common guillemots *Uria aalge* at colony in Shetland during the pre-breeding season. *Seabird* 30: 51-62. https://doi.org/10.61350/sbj.30.51

Trevail, A. M., Wood, H., Carr, P., Dunn, R. E., Nicoll, M. A., Votier, S. C. & Freeman, R. 2023. Multi-colony tracking reveals segregation in foraging range, space use, and timing in a tropical seabird. *Marine Ecology Progress Series* 724: 155-165. https://doi.org/10.3354/meps14479

Tremblay, F., Choy, E. S., Whelan, S., Hatch, S. & Elliott, K. H. 2024. Time-energy budgets outperform dynamic body acceleration in predicting daily energy expenditure in kittiwakes, and estimate a very low cost of gliding flight relative to flapping flight. *Journal of Experimental Biology* 227(21): jeb247176. https://doi.org/10.1242/jeb.247176

Wagner, R. H. 1999. Sexual size dimorphism and assortative mating in Razorbills (*Alca torda*). The *Auk* 116: 542-544. https://doi.org/10.2307/4089388

Supplementary materials

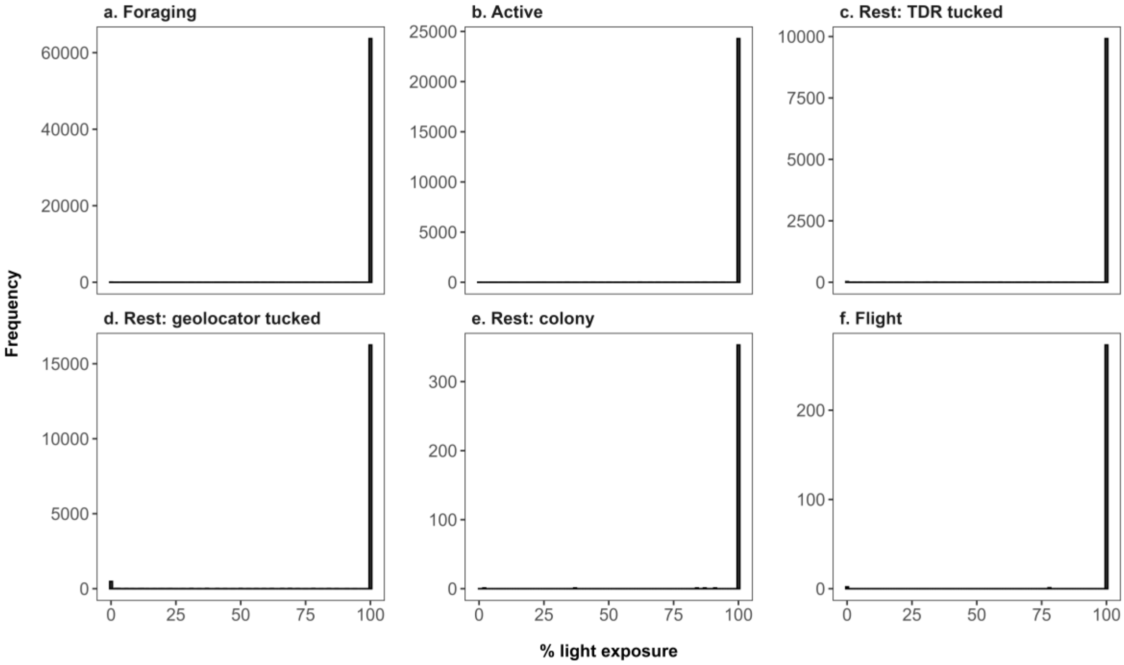

Figure S1. Histogram of percentage light exposure of the geolocator device during each behaviour, where behaviours were allocated using dual-deployed time-depth recorder and light-immersion data (Buckingham *et al.* 2023).

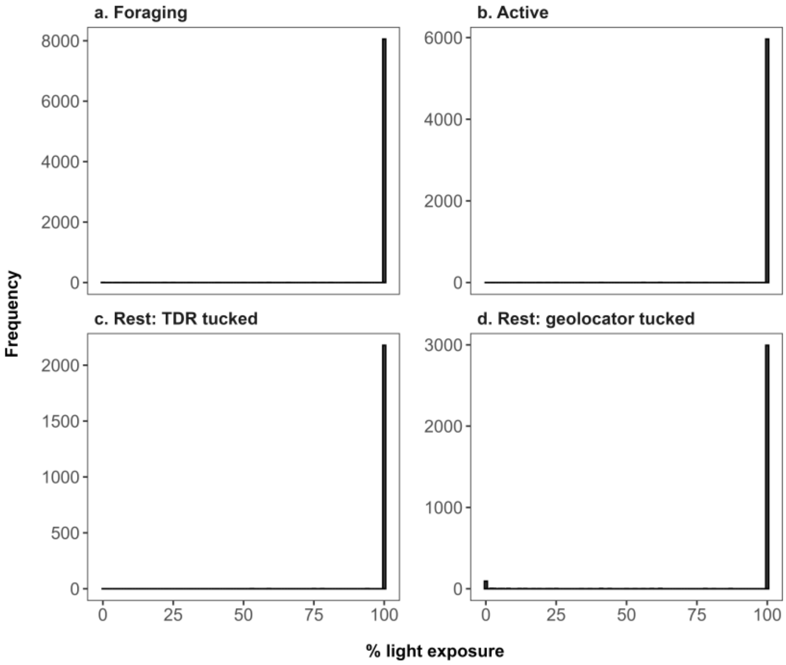

Figure S2. Histogram of percentage light exposure of the geolocator device during each behaviour, where behaviours were allocated using dual-deployed time-depth recorder and light-immersion data (Buckingham *et al.* 2023), during the expected post-breeding moult (16 August to 15 September).

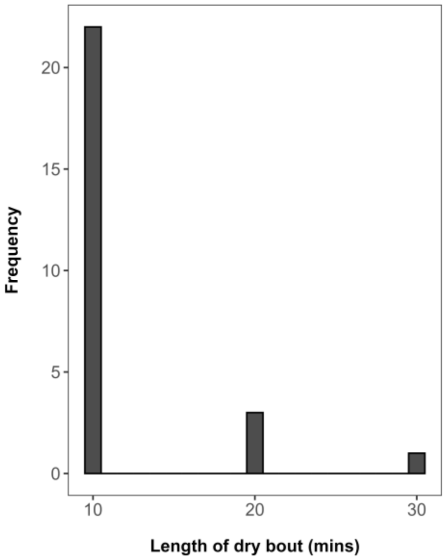

Figure S3. Histogram of the length of each dry bout defined using the dual-logger method after leaving the breeding colony and before the first observed colony attendance on the Isle of May (21 October; Bennett *et al.* 2024), used to inform the maximum length of flight in our behavioural allocation method.