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Modelling and mapping how common guillemots balance their energy budgets over a full annual cycle

Ruth E. Dunn[1,2] | Jonathan A. Green[1] | Sarah Wanless[3] | Mike P. Harris[3] | Mark A. Newell[3] | Maria I. Bogdanova[3] | Catharine Horswill[4,5,6] | Francis Daunt[3] | Jason Matthiopoulos[7]

[1]School of Environmental Sciences, University of Liverpool, Liverpool, UK; [2]Lancaster Environment Centre, Lancaster University, Lancaster, UK; [3]UK Centre for Ecology & Hydrology, Penicuik, UK; [4]ZSL Institute of Zoology, London, UK; [5]Centre for Biodiversity and Environmental Research, Department of Genetics, Evolution and Environment, University College London, London, UK; [6]Department of Zoology, University of Cambridge, Cambridge, UK and [7]Institute of Biodiversity Animal Health & Comparative Medicine, University of Glasgow, Glasgow, UK

Correspondence
Ruth E. Dunn
Email: ruthelizabethdunn@gmail.com

Abstract

1. The ability of individual animals to balance their energy budgets throughout the annual cycle is important for their survival, reproduction and population dynamics. However, the annual cycles of many wild, mobile animals are difficult to observe and our understanding of how individuals balance their energy budgets throughout the year therefore remains poor.

2. We developed a hierarchical Bayesian state-space model to investigate how key components of animal energy budgets (namely individual energy gain and storage) varied in space and time. Our model used biologger-derived estimates of time-activity budgets, locations and energy expenditure to infer year-round time series of energy income and reserves. The model accounted for seasonality in environmental drivers such as sea surface temperature and daylength, allowing us to identify times and locations of high energy gain.

3. Our study system was a population of common guillemots *Uria aalge* breeding at a western North Sea colony. These seabirds manage their energy budgets by adjusting their behaviour and accumulating fat reserves. However, typically during severe weather conditions, birds can experience an energy deficit over a sustained period, leading to starvation and large-scale mortality events.

4. We show that guillemot energy gain varied in both time and space. Estimates of guillemot body mass varied throughout the annual cycle and birds periodically experienced losses in mass. Mass losses were likely to have either been adaptive, or due to energetic bottlenecks, the latter leading to increased susceptibility to mortality. Guillemots tended to be lighter towards the edge of their spatial distribution.

5. We describe a framework that combines biologging data, time-activity budget analysis and Bayesian state-space modelling to identify times and locations of high

energetic reward or potential energetic bottlenecks in a wild animal population. Our approach can be extended to address ecological and conservation-driven questions that were previously unanswerable due to logistical complexities in collecting data on wild, mobile animals across full annual cycles.

1 | INTRODUCTION

Energy is a vital requirement in supporting an individual's basic functioning and maintenance. Animals need to maintain a positive energetic balance to survive and reproduce (Tomlinson et al., 2014). As such, variation in the ability of organisms to maintain an energetic balance (via energy intake, body reserves and energy expenditure) drives population dynamics and animal distributions (Bonn et al., 2004). In their efforts to acquire energy, animals experience variation in the energetic cost of movement according to environmental conditions, defined as 'energy landscapes' (Shepard et al., 2013; Wilson et al., 2021). More recently, the concept of 'energyscapes' has been expanded to also encompass spatial variation in individual energetic requirements as a function of environmental conditions (Amélineau et al., 2018). For organisms that inhabit seasonal environments, energyscapes can be strongly heterogeneous; animals experience pronounced seasonal variation in environmental conditions, climatic events, costs of movement, food availability and predator abundances (Gaynor et al., 2019; Varpe, 2017). The current phenomenon of global environmental change has the potential to alter seasonal energyscapes via changes in climatic conditions, shifts in species distributions and altered trophic interactions (Lauria et al., 2012; Perry et al., 2005). Maintaining an energy balance, as opposed to facing energetic bottlenecks (where supply does not meet demand), across these changing conditions is critical to survival (Clairbaux et al., 2021; Fort et al., 2009). Researching the mechanisms through which wild animals balance their energy budgets is therefore a priority (Lewison et al., 2012; Tomlinson et al., 2014). However, few studies have been able to investigate how wild animals allocate energy throughout their annual cycles (Swift et al., 2020) as year-round data, in particular, have been lacking (Marra et al., 2015).

Innovations in biologging technology have increasingly enhanced our ability to record locational and activity data for individuals over full annual cycles (Bograd et al., 2010; Hussey et al., 2015). However, despite these advances we still know relatively little about how the energy budgets of wild animals, as well as their propensity to experience potential energetic bottlenecks, might vary in time and space throughout their annual cycle (but see Green et al., 2009; Swift et al., 2020). Due to logistical complexities, measuring the energetics of wild animals, even over short time-scales, can be challenging. Our understanding is therefore currently limited primarily to measures of individual energy expenditure and, more rarely, energyscapes,

as opposed to energetic income and reserves. Previous studies that have derived year-round energy expenditure estimates have focused on time-activity budgets (Dunn et al., 2020; Pelletier et al., 2020), the calculation of overall dynamic body acceleration (a proxy for energy expenditure; Efrat et al., 2019; Flack et al., 2016), heart rate monitoring (Halsey et al., 2019), and mechanistic modelling using the tool, Niche Mapper™ (Amélineau et al., 2018; Fort et al., 2009). However, to fully understand both temporal and spatial variation in how animals either manage their energy budgets or face potential bottlenecks, it is also important to understand how they gain and store energy, as well as how their environment and life-history priorities influence this (Nwaogu & Cresswell, 2016). Analytical developments (such as hierarchical Bayesian state-space models) allow the reconstruction of hidden time series of ecological and physiological variables that are otherwise difficult to directly and continuously measure throughout animal annual cycles (Patterson et al., 2008; Russell et al., 2013). Here, we use these models to mechanistically link time-activity budget data with environmental drivers, thereby reconstructing year-round variation in the individual energy gain, body reserves and consequent potential threats to survival of a wild, mobile population of animals.

We developed our approach to reconstructing year-round time series of animal energy income and reserves using the common guillemot *Uria aalge* (hereafter 'guillemot') as a study system. Guillemots are an abundant, medium-sized (*c.* 1 kg), diving seabird from the Alcidae family that breed once per year at colonies around the coasts of the North Atlantic and Pacific oceans (Gaston & Jones, 1998). We studied guillemots from a breeding colony on the Isle of May, Scotland (Figure 1a), the annual cycle of which is outlined in Figure 1b. After the breeding season, Isle of May guillemots typically migrate into the North Sea and English Channel (Dunn et al., 2020), although one individual has repeatedly been recorded making an extreme migratory journey to the Barents Sea (3,000 km from the breeding colony; Harris et al., 2015). Annual survival in this population is typically high (*c.* 90%; Reynolds et al., 2011); surviving individuals adjust their migratory behaviour, make periodic returns to the colony, and manage their time-activity and energy budgets in the face of potential constraints such as reduced sea surface temperatures and daylengths during winter (Dunn et al., 2020).

Throughout their annual cycles, guillemots exhibit seasonal variations in body mass; healthy Scottish birds lose mass over the breeding season and accumulate fat reserves during their post-breeding
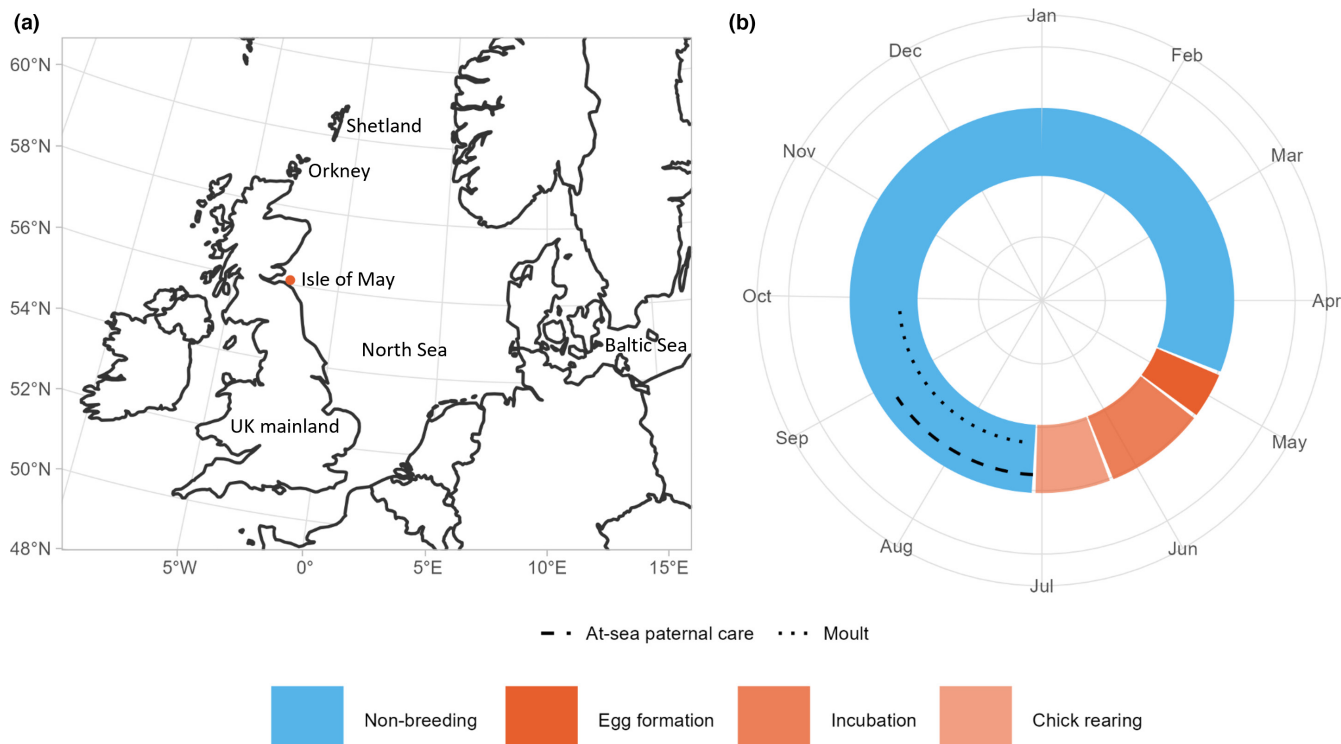
FIGURE 1 (a) Location of the Isle of May study site (orange circle) as well as other key locations, mentioned within the Results. (b) Diagram of the annual cycle of a breeding common guillemot from the Isle of May

flightless moult period and the winter (Harris et al., 2000). Mass loss during the breeding season may be adaptive and can lead to increased flight efficiency, dive performance and savings in energy expenditure for breeding guillemots (Croll et al., 1991; Elliott et al., 2008). Furthermore, the accumulation of energetic reserves to reduce the risk of energetic bottlenecks and starvation during potentially adverse winter feeding conditions, may also lead to seasonal mass changes (Harris et al., 2000). Despite these adaptive responses to physiological and environmental constraints, North Sea guillemots are periodically involved in large-scale mortality events, or 'wrecks', that typically occur during severe weather in the winter (Harris & Wanless, 1996). Birds that die in these wrecks are usually emaciated, indicating that they have been in negative energy balance over a sustained period, most likely due to being unable to feed sufficiently, resulting in progressive, extreme and irreversible mass loss (Clairbaux et al., 2021; Debacker et al., 2000). As long-lived species with low reproductive rates, delayed maturity and high survival rates, the population dynamics of guillemots is highly sensitive to changes in adult mortality, such as that caused by wrecks (Ricklefs & Wikelski, 2002).

In this study, we used biologging data to estimate the year-round daily time-activity budgets, locations and energy expenditure of individual guillemots that survived an annual cycle. Next, we developed a state-space model around these data to reconstruct hidden time series of individual energy gain and body mass to investigate whether we could infer how energy budgets might vary in time and space over the annual cycle. We used this state-space model to address three key questions: (a) Where and when does variation in guillemot energy gain occur throughout the annual cycle? (b) How

do relevant environmental drivers such as sea surface temperature, daylength, latitude, longitude and distance from the coast influence year-round energetic gain? (c) Where and when does the Isle of May population of guillemots experience energetic constraints, reflected through reductions in mass, which may increase susceptibility to mortality? By creating this model and addressing these questions, we sought to develop an approach that can be used to identify times and areas of both high energetic reward, as well as potential energetic bottlenecks in wild, mobile animals.

2 | MATERIALS AND METHODS

To reconstruct the hidden annual time series of daily individual energetic gain and body mass for adult guillemots (not accounting for that 'gained' for the chick), we constructed a hierarchical Bayesian state-space model that combined biologger-derived estimates of location, activity and energy expenditure with prior information from other studies. Below, we provide an overview of the data used and describe the structure of the state-space model. All data processing and analyses were performed using R version 4.0.2 (R Core Team, 2020) and JAGS (Plummer, 2003).

2.1 | Study site, biologging and environmental data

Fieldwork took place on the Isle of May National Nature Reserve, Scotland (56°11′N, 02°33′W, Figure 1a). In June 2016, 30 adult

guillemots that were brooding young chicks were captured at their breeding sites using a noose pole. Although all birds were chick-rearing and were therefore likely high-quality individuals, they were otherwise chosen opportunistically with no selection on mass, age or sex. Global location sensing loggers (GLS; MK3006 from Biotrack, UK) that measured light, temperature and conductivity were attached to the birds using Darvic leg-rings under British Trust for Ornithology and NatureScot licences (licence number C/4671; combined mass 3.5 g, or <0.4% of the mass of the adults on which they were deployed). During the two subsequent breeding seasons, birds were recaptured using the same method and the loggers removed (80% overall retrieval rate; $n_{2017} = 21$; $n_{2018} = 3$). We therefore only obtained data from birds that survived the annual cycle. Nearly all individuals were weighed to the nearest gram using a Pesola spring balance at logger deployment and retrieval ($n_{deployment} = 29$; $n_{retrieval} = 24$) and the handling process took <5 min each time. Of the retrieved loggers, 17 (71%) recorded data over the entire annual cycle and were used within the analyses. All procedures were conducted in accordance with relevant UK guidelines and regulations and were approved under research licences issued by NatureScot (licence number MON/RP/181 and its predecessors).

Daily energy expenditure in Alcidae seabirds, or auks, varies throughout the annual cycle in relation to daylength and sea surface temperature (Dunn et al., 2020; Fort et al., 2009). Additionally, migratory strategies and wintering areas can also influence the energetic costs experienced by seabirds (Pelletier et al., 2020). To investigate the influence of sea surface temperature, daily location, number of daylight hours and distance to the coastline on guillemot energetics throughout the annual cycle, we extracted these variables for each observation recorded by the loggers. Estimation of locations was done following the same methods as Dunn et al. (2020) for the

same study population, and is further detailed in the Supporting Information (S1). Covariate data were also extracted using previously described approaches for this species and study site (Supporting Information S1). Specific predictions for the response of energetic gain to these environmental drivers are summarised in Table 1.

Daily time-activity budgets were estimated from conductivity data, designed for wet/dry determination, using approaches developed for this species and study site (Supporting Information S2), based on similar classification approaches used in previous studies of auk activity budgets (e.g. Dunn et al., 2020; Elliott & Gaston, 2014; Fayet et al., 2017; Linnebjerg et al., 2014). We combined the resultant daily time-activity budgets (formed of the time spent each day in flight F, resting R, active on water A and foraging D) with sea surface temperature T and estimates of activity-specific energetic costs. Activity-specific energetic costs were extracted from Elliott et al. (2013), converted into kilojoules per day, and corrected for the effect of temperature as in Elliott and Gaston (2014). Daily energy expenditure (E in kJ) of adult guillemots throughout the annual cycle was therefore determined as:

$$E_{i,t} = 33.12\,R_{i,t} + 507.6\,F_{i,t} + (113 - 2.75\,T_{i,t})A_{i,t} + 97.2\,D_{i,t}. \quad (1)$$

Here, subscripts i and t denote individual and day, respectively, where t ranges from 1 to 364 and corresponds to a time series from 26th June 2016 to 24th June 2017.

2.2 | Bayesian state-space modelling

We developed a Bayesian state-space model to estimate the hidden (latent) time series of adult guillemot individual energy gain and

TABLE 1 Predictions of hypotheses of the influence of environmental drivers on the individual energetic gain of adult common guillemots from the Isle of May throughout the annual cycle

Parameter	Prediction	Citations supporting the prediction
Sea surface temperature	Alternative predictions: (a) individual energy gain will be higher at low sea surface temperatures as birds will need to acquire more energy to meet the heightened costs of thermoregulation; (b) individual energy gain will be higher at high sea surface temperatures as birds will need to acquire more energy to recover from the heightened costs of the breeding season	Croll and McLaren (1993); Dunn et al. (2020)
Number of daylight hours	Individual energy gain will be higher on shorter days due to birds foraging more during the winter months to maintain high body condition during colder environmental conditions	Dunn et al. (2019)
Longitude	Alternative predictions: (a) individual energy gain will be positively influenced by longitude as birds migrate further east from the Isle of May, into the North Sea, to gain access to more profitable foraging areas; (b) individual energy gain will be negatively influenced by longitude as birds move away from favourable feeding areas in relatively coastal locations	Jensen et al. (2011)
Latitude	Individual energy gain will be higher at lower latitudes, due to moulting and wintering Isle of May guillemots foraging in the southern North Sea	Harris et al. (2015); St. John Glew et al. (2018)
Distance to coastline	Individual energy gain will be higher closer to the coast as lesser sandeels *Ammodytes marinus* (a key component of guillemot diet) are associated with sandbanks which are often in shallow, relatively coastal waters	Jensen et al. (2011)

body mass. This biological part of the state-space model describes a Markov process where the two hidden states evolve at daily time intervals, given the previous states, process variability and biological parameters (Jonsen et al., 2005). We were ultimately interested in estimating $M_{i,t}$ and $G_{i,t}$, the mass M and daily individual energy gain G of individual i at day t.

An individual's mass on a given day $M_{i,t+1}$ was defined using a random-walk model as follows:

$$M_{i,t+1} \sim N\left(\mu_{i,t+1}, \tau_{i,t+1}\right). \qquad (2)$$

The precision of this normal distribution τ reflects the physiological variation around the expectation μ, which we assigned from a normal distribution with a mean of 0.046 and standard deviation of 0.02 (Table 2). We assumed a mean physiological variation of $\pm 1\%$ of body mass, as there is no evidence to suggest that individuals would adjust conversion rates between food, energy and body mass at a daily timescale (Halsey, 2018). The expectation μ of this distribution reflects an individual's mass on the previous day plus a change in mass that was dependent on whether there was an energy surplus or deficit:

$$\mu_{i,t+1} = M_{i,t} + V\left(G_{i,t} - E_{i,t}\right). \qquad (3)$$

We assumed that excess lipids were transferred to body reserves while excess protein was excreted or used in other metabolic pathways (Green et al., 2007). In the closely related Brünnich's guillemot *Uria lomvia*, lipids accounted for 35.25% of mass lost across a breeding season (Elliott et al., 2008). The energetic density of lipid is 39.3 kJ/g, and therefore, assuming that birds in energy deficit use fat stores as the primary source of metabolic energy, this would equate to a mass change value V of 0.072 g lost per kJ. We also assumed that birds experiencing an energetic surplus put excess lipid into their fat stores and therefore gained mass at the same rate. We assigned a gamma prior distribution with a mean of 0.072 and a standard deviation of 0.001 (Table 2) to the mass change parameter V, to account for uncertainty.

To describe stochasticity in daily individual energy gain $G_{i,t}$ we used a gamma model, suitable for a continuous, non-negative variable that offers parametric control for overdispersion. Here, the state process equation described the mean daily individual energy gain ($\overline{U}$) for the ith individual on day t as a log-linear function of the environmental covariates, sea surface temperature S, number of daylight hours L, longitude X, latitude Y, and distance to coastline C:

$$\overline{U}_{i,t} = D_{i,t}\exp\left(r_0 + r_1 S_{i,t} + r_2 L_{i,t} + r_3 X_{i,t} + r_4 Y_{i,t} + r_5 C_{i,t}\right), \qquad (4)$$

Here, the intercept r_0 corresponds to the individual energy gain per hour which was then scaled up by $D_{i,t}$, the number hours spent foraging on day t. To prevent modelling negative energy gain, we assumed that all birds spent no less than 1 min foraging each day. We assigned a gamma prior to the intercept parameter, where the mean and standard deviation (143 and 100 kJ/hr, respectively; Table 2) were generated by summing the amount of time per hour foraging that was spent actively engaged in prey capture (40 min when accounting for

inter-dive intervals), the number of prey items caught per minute foraging (0.8 ± 0.4 items; Thaxter et al., 2013), the energetic density of prey items (5.8 ± 0.5 kJ; Wanless et al., 2005), and the nitrogen-corrected metabolisable energy coefficient of lesser sandeels *Ammodytes marinus* (77.52 ± 1.60%; Hilton et al., 2000). The large amount of uncertainty in this prior allowed energy gain rates to vary throughout the annual cycle, thereby allowing flexibility without imposing arbitrary constraints. Furthermore, Isle of May guillemots feed at a consistently high trophic level throughout the summer (Daunt et al., 2008), autumn and winter (St. John Glew et al., 2018), with year-round diet likely to be dominated by small fish (Blake et al., 1985; Wanless et al., 2005). Should further information on diet and prey energy density become available, future studies could incorporate this. The coefficient values r_1, r_2, r_3, r_4 and r_5 were assigned from normal prior distributions centred at 0 (Table 2), thus expressing the null hypothesis of no effect from each covariate (Table 1).

We used a gamma link function to incorporate residual environmental stochasticity around the mean daily energy gain estimated for each individual:

$$G_{i,t} \sim \text{Gamma}\left(r_{i,t}, \lambda_{i,t}\right), \qquad (5)$$

The shape r and rate λ of this stochastic process were written as functions of the estimated daily individual energy gain $\overline{U}$ (Equation 4), and the precision φ of this process, representing residual environmental stochasticity around the mean. To assign precision, we used a normal prior distribution that was precautionarily wide, that is, an expectation of 500 kJ/day and a standard deviation of 100 kJ/day (Table 2).

The random walk model outlined in Equation 2 allows changes in mass to be constrained by the biological priors; however, the overall mass that an individual can reach is, in principle, unconstrained. To account for biological constraints on both minimum and maximum mass, we wanted to penalise the likelihood when the overall mass of the animal went above or below a certain maximum and minimum mass, respectively. Attempting this in conjunction with Equation 2 did not work during model fitting, due to needing a smooth central tendency, rather than a truncation. Therefore, we introduced an additional constraint to $M_{i,t}$:

$$M_{i,t} \sim N\left(1025, 2.21 \times 10^{-5}\right). \qquad (6)$$

These values were used as 1,025 g was the midpoint between the heaviest guillemot mass recorded M_{max} (1,450 g; Harris et al., 2000) and the lightest sustainable body mass M_{min} (600 g; Grogan et al., 2014). The value that we used for the precision (2.21×10^{-5}) was calculated as follows:

$$\frac{1}{\sigma_p^2}, \text{where } \sigma_p = \frac{\left(M_{max} - M_{min}\right)}{4} = 2.21 \times 10^{-5}, \qquad (7)$$

All models were fitted using JAGS (Plummer, 2003), using the *runjags* interface in R (Denwood, 2016). We ran our models with a burn-in of 20,000 and for 30,000 iterations to achieve convergence.

TABLE 2 Prior distributions for the parameters used to model adult guillemot mass and daily individual energy gain throughout the annual cycle. Gamma distributions are expressed in terms of shape and rate and normal distributions are expressed in terms of mean and precision

Output	Variable	Parameter	Prior
Mass	Precision	τ	$\sim \text{gamma}(4.65, 0.94)$
	Mass change value	V	$\sim \text{gamma}(20793.64, 288400)$
Individual energy gain	Environmental stochasticity	φ	$\sim N(500, 0.0001)$
	Intercept	r_0	$\sim \text{gamma}(1.161, 0.234)$
	Sea surface temperature	r_1	$\sim N(0, 0.01)$
	Daylight length	r_2	$\sim N(0, 0.01)$
	Longitude	r_3	$\sim N(0, 0.01)$
	Latitude	r_4	$\sim N(0, 0.01)$
	Distance to coastline	r_5	$\sim N(0, 0.01)$

The JAGS code is presented in Supporting Information S3. To assess the sensitivity of our model to the biologically informed priors used, we inflated the prior distributions of τ and V (Table 2) by doubling their standard deviations and comparing the outputs with our original results (Supporting Information S5). To investigate the effect of the environmental variables (sea surface temperature, daylight hours and distance to coastline) on year-round individual energetic gain, we used the Deviance Information Criterion (Burnham & Anderson, 2002) to perform model selection (via backward elimination) on models containing variations of the linear predictor $\overline{U}_{i,t}$ (Equation 4; see Supporting Information Table S4). Convergence of these models was evaluated via visual inspection of the MCMC chains.

2.3 | Identification of times and locations of low mass and high energetic gain

The final model used to reconstruct annual time series of adult body mass M and individual energy gained G included sea surface temperature, daylight hours, latitude and distance to coastline. We then extracted one value of body mass each week, calculated mean daily energy gain per week and used these time series to visualise times and locations where birds experienced low masses and subsequent potential higher susceptibility to mortality. The lowest mass recorded during breeding season weighing at the Isle of May ($n = 264$ birds weighed between 2014 and 2018) was 800 g and we therefore highlighted weekly intervals where the 95% Bayesian credible interval (CRI) for mass included the value of 800 g, indicative of low body mass. Finally, we mapped spatial variation in average mass and individual energy gain using the R packages SP (Pebesma & Bivand, 2005), RASTER (Hijmans, 2021) and PLOTKML (Hengl et al., 2015) and 100 km grid squares to reflect the

spatial resolution of the geolocation data. When visualising the spatial distribution of energy gain, we mapped the sum of the total individual energy gained by all 17 individuals in each grid square during each season. When visualising the locations where birds experienced low masses, we mapped the mean mass of the individuals located within each grid square during each season.

3 | RESULTS

Our model reconstructed annual time series of daily body mass and individual energy gain of 17 adult guillemots from 26th June 2016 to 24th June 2017. Of the five covariates investigated within our models, model selection indicated that sea surface temperature, the number of daylight hours, latitude and distance from the coast influenced energy gain, whereas longitude did not (Supporting Information Table S5). The Bayesian credible intervals (CRIs) of the posterior distribution of sea surface temperature suggested that there was a small but consistent positive effect of this covariates on guillemot energetic gain, whereas day length, latitude and distance from the coast had consistent negative effects. For example, for an increase of 1°C in sea surface temperature, hourly individual energy gain energy increased by 4%, or 12 kJ (CRI = 7–17 kJ), from the mean hourly energy acquisition (269 kJ; CRI = 261–274 kJ). In contrast, being 1-degree further north would produce a decrease of 9 kJ (CRI = 7–14 kJ) and being 1 km further from the coastline would produce a decrease of 10 kJ (CRI = 7–14 kJ) per hour. Similarly, hourly individual energy gain was expected to decrease by 31 kJ (CRI = 27–34 kJ) with each additional hour of daylight. Thus, guillemots tended to gain more energy in relatively warmer waters, on shorter days, while further south and closer to the coast.

Estimates of adult guillemot individual energy gain varied temporally over the course of the annual cycle, both within individuals and between individuals (Figure 2a). Daily individual energy gain estimates ranged from a mean of 721 kJ/day for one individual for the week of the 25th–31st May 2016, to 3,567 kJ/day by another individual between 21st and 27th July 2016. There was high variability in daily energy gain between individuals, and values tended to be lower during May and June, when guillemots incubate their eggs and rear their chicks (Figure 1b), and were higher during August, immediately following the breeding season (Figure 2b).

In addition to varying temporally, individual energy gain by guillemots also varied spatially over the annual cycle (Figure 3). Throughout their annual cycle, guillemots that breed on the Isle of May foraged within a large area that extends across the North Sea; however, within this region, areas of high energy gain were evident (Figure 3). These high energy gain areas were predominantly located in the north-western North Sea, close to the coasts of eastern Scotland and north-east England (Figure 3). Seasonal changes in the spatial distribution of total energy gain were largely driven by changes in the time that birds spent foraging within the different areas (Figure S6). Our sensitivity analysis revealed minimal change
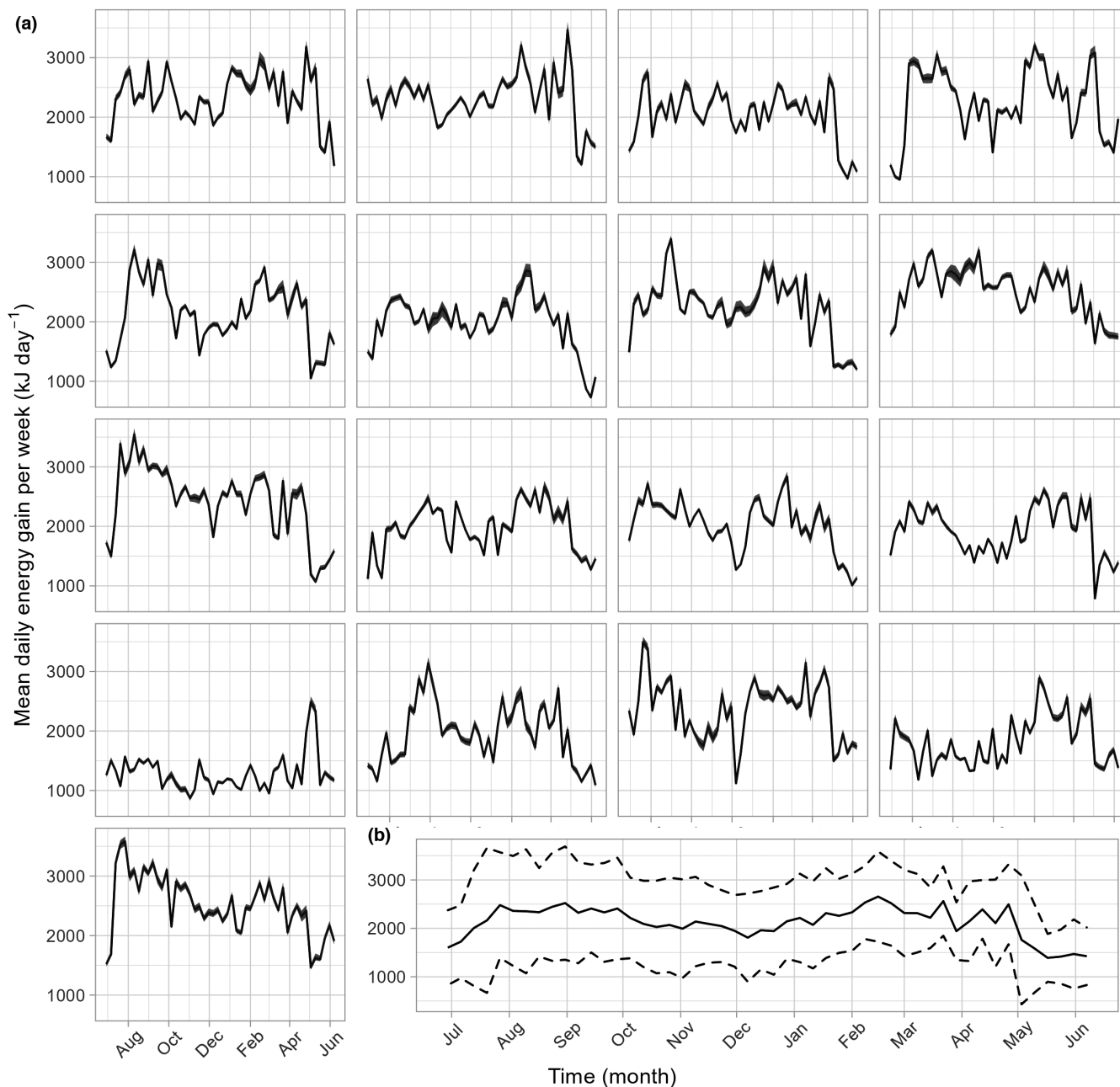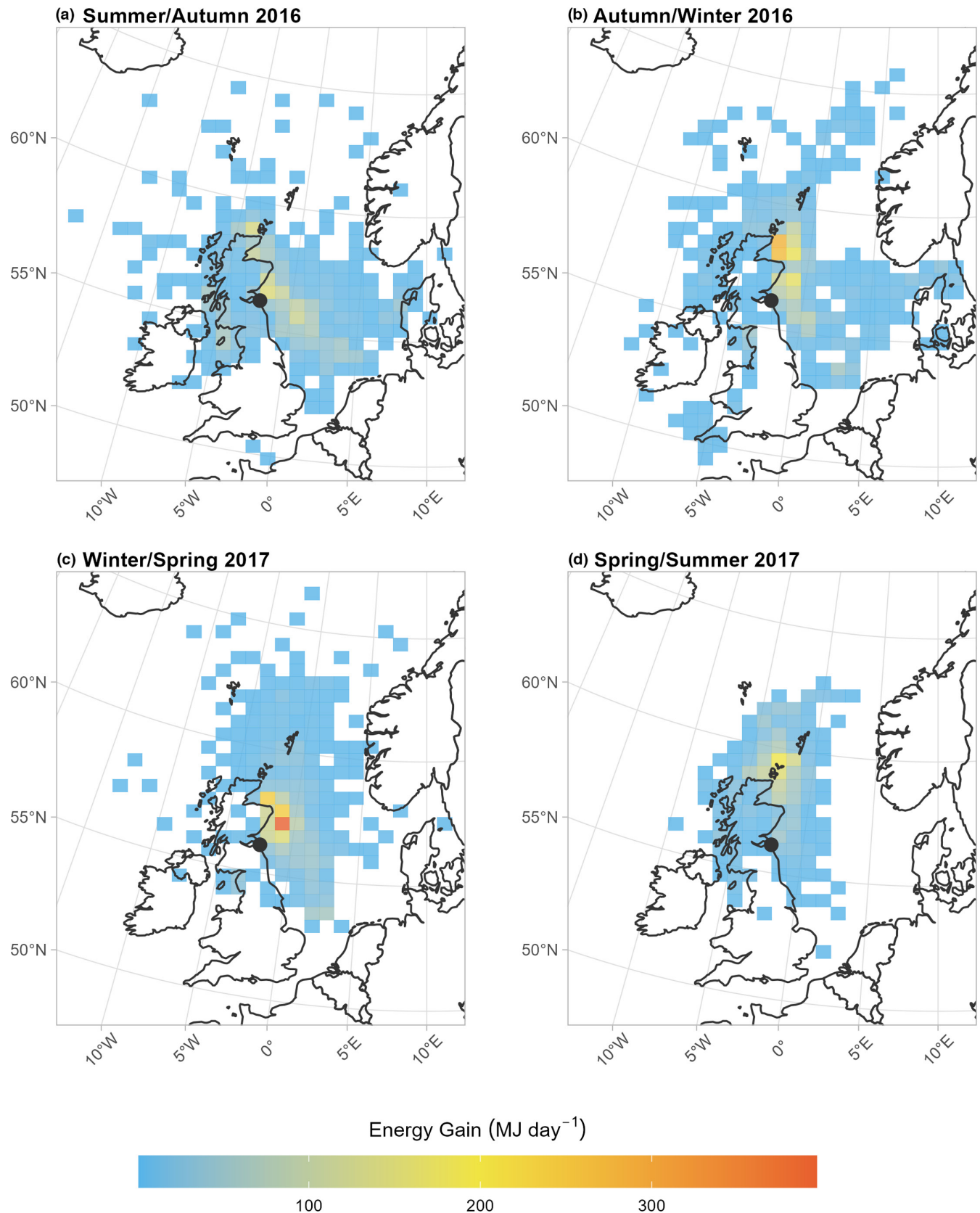
FIGURE 2 (a) Reconstructed fluctuations in the daily individual energy gain per week of 17 adult common guillemots from the Isle of May throughout the 2016–2017 annual cycle. Values of daily individual energy gain are means, calculated at weekly intervals. The solid lines show the posterior median daily individual energy gain, and the shaded areas show its associated uncertainty (95% Bayesian credible intervals). (b) The mean population energy gain per week, with the standard deviation between individuals indicated with dashed lines

to the individual energy gain trajectories when we inflated the prior distributions of τ and V (Figure S5.1) or to the distribution of where guillemots gained energy (Figure S5.2), suggesting that these results were robust.

In general, we detected no obvious temporal trend in guillemot body mass over the course of the annual cycle (Figure 4a). Instead, guillemots tended to maintain a relatively consistent body mass from week to week (Figure 4a). Despite this, there was variation between animals in the timing and magnitude of variation around this generally consistent mass. Indeed, all 17 individuals

experienced at least one time period when the 95% Bayesian credible interval (CRI) for mass included the value of 800 g (the lowest mass recorded during the breeding season at the Isle of May; Figure 4a). These periods of potential low mass occurred throughout the year, but in 2016–2017 were most frequent in July, September, March and April (Figure 4b). The greatest mass loss estimated for an individual was 241 g over the 7-day period preceding 20th July 2016. The lack of an obvious temporal pattern in year-round body mass was retained when we inflated our prior distributions in the sensitivity analysis (Figure S5.3).

FIGURE 3 Where adult common guillemots from the Isle of May gained energy throughout the annual cycle. Spatial distribution (100 km resolution) of estimates of total energy gained (MJ/day) from the environment by all 17 guillemots from the Isle of May (illustrated with a black circle) in (a) 01/07/2016–September 30, 2016, (b) 1/10/2016–December 31, 2016, (c) 01/01/2017–March 31, 2017 and (d) 01/04/2017–07/06/2017. Values were calculated by summing the total individual energy gained by all 17 individuals within each cell during each season
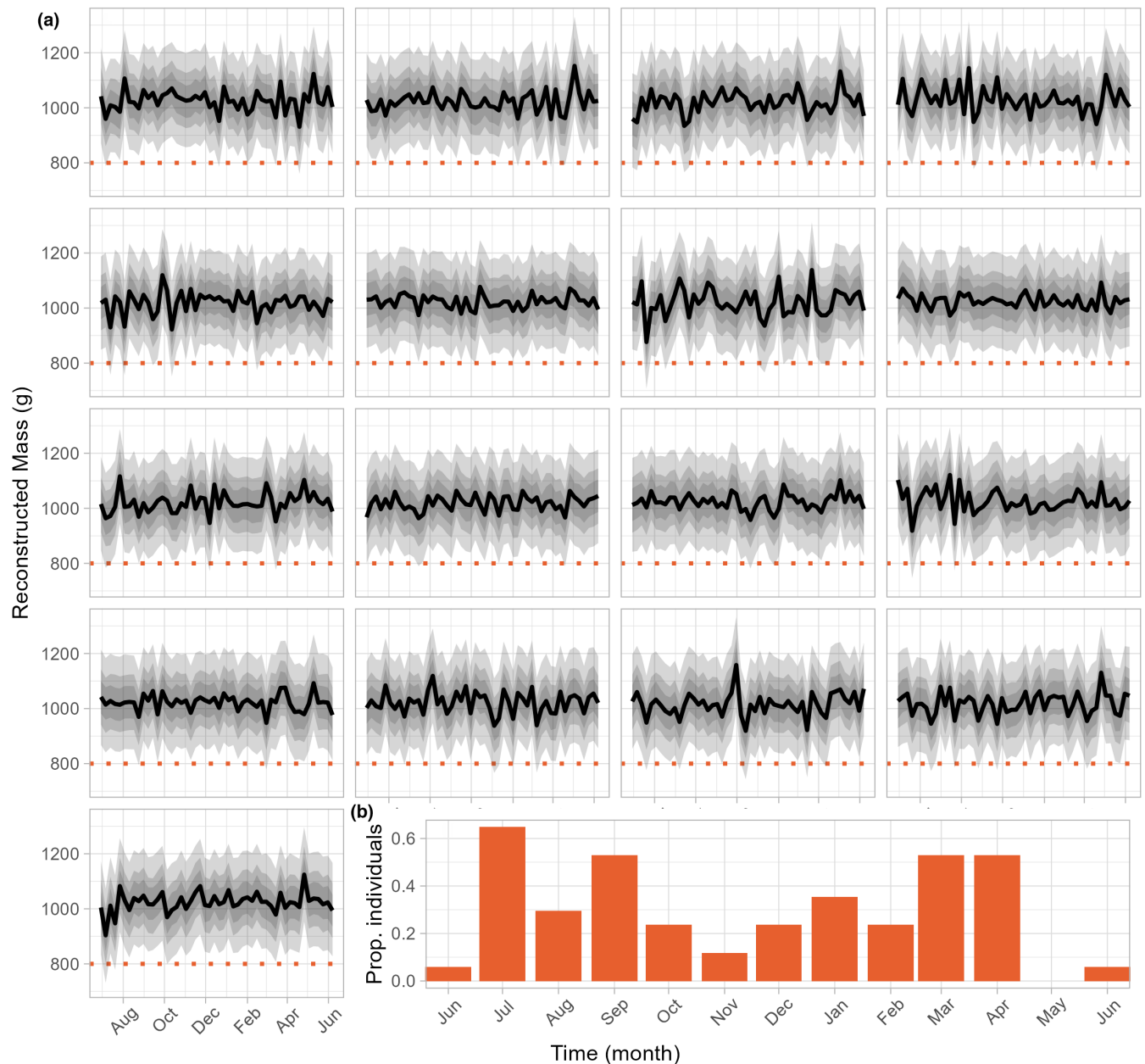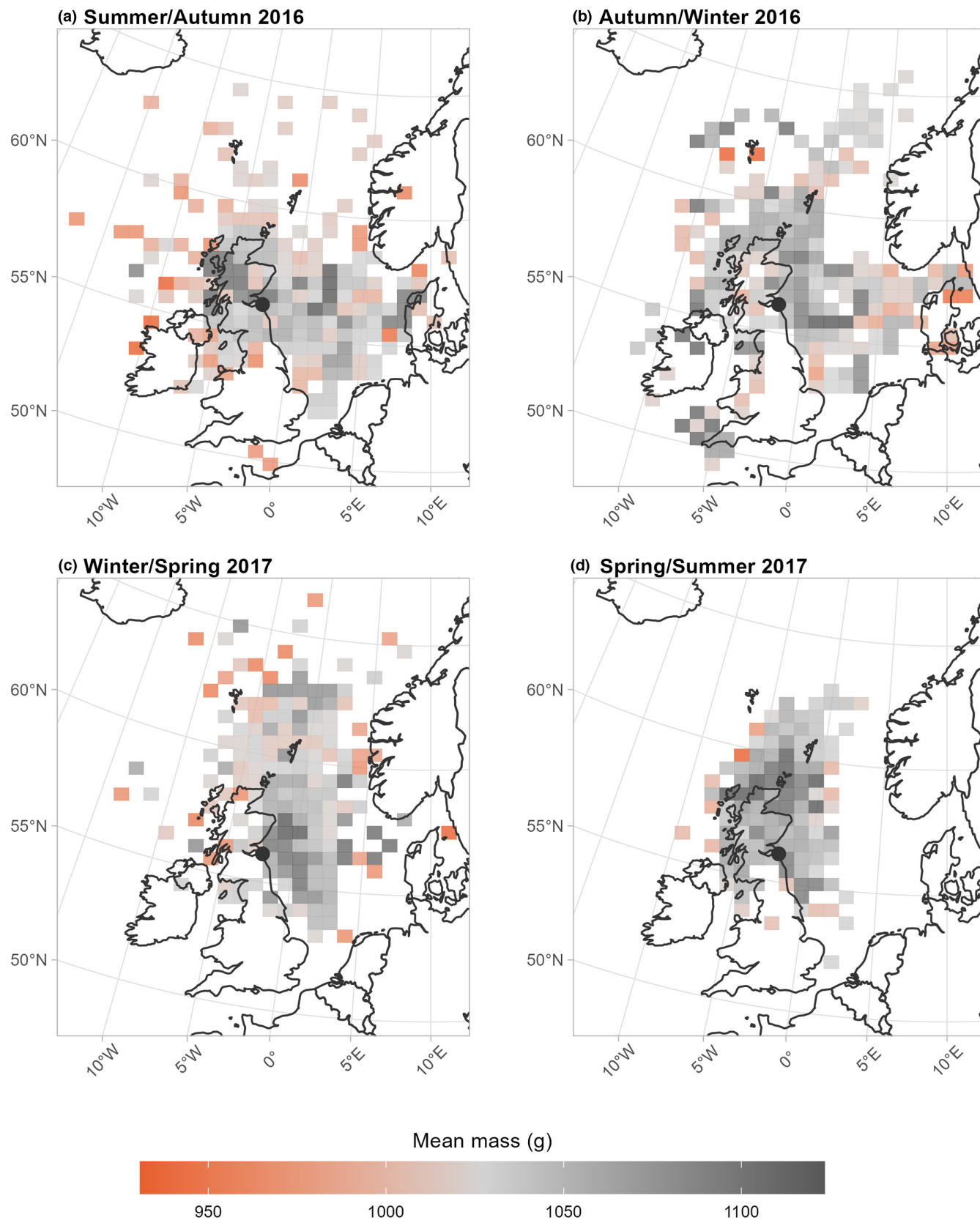
FIGURE 4 (a) Reconstructed fluctuations in the estimated body masses of 17 common guillemots from the Isle of May at weekly intervals across the 2016–2017 annual cycle. The thick lines show the posterior median daily body mass and the shaded areas show its associated uncertainty (including 50%, 75% and 95% Bayesian credible intervals, in order from darkest to lightest). The dashed orange lines illustrate 800g, the lowest mass recorded during breeding season weighing at the Isle of May (*n* = 264 birds weighed between 2014 and 2018). (b) The proportion of individuals where the 95% Bayesian credible interval (CRI) for mass included the value of 800g each month across the annual cycle

Over the annual cycle, guillemots from the Isle of May were distributed widely in the North Sea and lower masses occurred across the full range of this spatial distribution (Figure 5). Areas of low mass were often towards the edge of the population's distribution and included northerly locations, areas between the North and Baltic Seas to the east, and the central and eastern North Sea during the autumn and winter (Figure 5a–c). Our sensitivity analyses revealed that when we inflated our prior distributions, the spatial pattern was broadly similar (Figure S5.4).

4 | DISCUSSION

We set out to investigate how, where and when the energy budgets of common guillemots varied over a full annual cycle. Although it is challenging to directly collect data on year-round energetics, particularly energetic income and storage, here we illustrate the potential to use routinely collected biologging data to estimate energy expenditure, via time-activity budget analysis, and subsequently reconstruct individual energy gain and mass change trajectories. We

(a) Summer/Autumn 2016

(b) Autumn/Winter 2016

(c) Winter/Spring 2017

(d) Spring/Summer 2017

Mean mass (g)

950   1000   1050   1100

FIGURE 5 Where adult common guillemots from the Isle of May experienced lower masses throughout the annual cycle. Distribution of the average mass (g) of 17 guillemots from the Isle of May (illustrated with a black circle) across their spatial distribution (100 km resolution) in (a) 01/07/2016–September 30, 2016, (b) 1/10/2016–December 31, 2016, (c) 01/01/2017–March 31, 2017 and (d) 01/04/2017–07/06/2017. Values are means of the masses of the individuals located within each cell during each season

recreated time series of energy gain and storage over a full annual cycle using a hierarchical Bayesian state-space model, thereby incorporating several items of expert knowledge in the form of Bayesian priors, while also increasing the inferential strength of the model by allowing it to be fitted to multiple individuals simultaneously. This approach allowed us to quantify how individual energetic gain and body mass varied over time and space. We therefore demonstrate an expansion of the concept of energyscapes that enables us to highlight times and locations of both favourable (high individual energy gain) and unfavourable (lower masses that could potentially reflect energetic bottlenecks and potential risk of mortality) conditions. The identification of key areas, both those of high importance for energy gain and those where organisms may face energetic bottlenecks, is a fundamental prerequisite for understanding year-round ecophysiology and the drivers of animal distributions.

Energyscapes are a mechanism through which to investigate the drivers of energetic costs to animals across the landscapes that they inhabit (Amélineau et al., 2018; Shepard et al., 2013). Here we illustrate that our approach can also highlight both seasonal and spatial variability in components of wild animal energetic budgets that are difficult to measure, namely individual energy gain and energy storage. For example, cold temperatures drive increased energy expenditure in guillemots (Burke & Montevecchi, 2018; Dunn et al., 2020) and have the potential to shape auk migration strategies and winter distributions (Fort et al., 2012). Here, we now show that seasonal variation in sea surface temperature can also influence individual guillemot energy gain, likely through the need to compensate for changes in thermoregulatory costs, as well as via potential impacts on the ecology of prey species. Additionally, although cost of movement is a key driver of ecological distributions within energyscape theory, whereby animals seek to minimise travel costs and maximise individual energy gain (Wilson et al., 2021), here we were able to directly visualise year-round distributions of guillemot energy consumption (Figure 3). Despite the location error associated with GLS loggers (c. 186 km; Phillips et al., 2004) and the possibility of misclassification of behaviours from saltwater immersion data, the locations of high energy gain identified through our modelling approach were biologically interpretable areas off the coast of eastern Scotland and north-east England (Figure 3). These high energy gain locations broadly overlapped with a sandeel fishery area that was closed to protect sandeel-dependent seabirds during their breeding seasons (Daunt et al., 2008), but is here revealed to be important to guillemots throughout the whole annual cycle. Investigating the spatial distribution of the food consumption of seabirds, and other marine top predators, throughout their annual cycles is important with regards to the conservation and management of marine resources worldwide (Brooke, 2004; Sherley et al., 2020). By applying our methodology to populations of other mobile, wild animals, it will become increasingly possible to generate temporally specific energy gain surfaces at a regional, and even global, level. Producing energy gain surfaces (like those in Figure 3) not only has benefits with regards to the management of both terrestrial and marine resources (Cury et al., 2011; Wood et al., 2019), but also has

ecological significance due to the dynamic interspecific and intraspecific competition pressures that occur as species and populations mix throughout their annual cycles (Buckingham et al., 2022; Frederiksen et al., 2012; González-Solís et al., 2007).

In addition to demonstrating the ability to identify times and locations of high energy gain, we also illustrate that our approach could be developed to investigate where, when and how individuals may undergo changes in mass. It was notable that all birds experienced periods of low mass throughout the year (Figure 4). In this study, our focus was highlighting when individuals might experience increased vulnerability to mortality over the annual cycle and we did this by identifying periods when guillemot mass predictions included the value of 800 g. This value could be adjusted in future to suit different species, populations, or in the light of any new evidence on mass thresholds. This being said, it is also important to consider adaptive mass loss, a key strategy employed by many seabirds during their breeding seasons to increase energetic efficiency (Croll et al., 1991; Norberg, 1981). Few birds experienced low masses during the peak of chick rearing in June (Figures 1b and 4), which is consistent with birds being more likely to abandon breeding than let adaptive mass loss approach a critical threshold (Drent & Daan, 1980). However, a high proportion of individuals experienced low masses in July (Figure 4), during the latter part of the breeding season (Figure 1), when birds may be experiencing energetic constraints due to the costs associated with rearing a chick (Dunn et al., 2018), or be struggling to recover from adaptive mass loss. Indeed, the late breeding period has previously been highlighted as a period when guillemot body mass and fat reserves are known to be at a minimum (Harris et al., 2000).

Locations where guillemots were lighter tended not to overlap with high energy gain areas and were instead at the edge of the birds' winter distributions (Figure 5). Periods of low mass were relatively common during September, when guillemots undergo a costly primary feather moult (Guillemette et al., 2007), and in March and April, when Isle of May guillemots spend an increasing amount of time at the colony, necessitating costly commuting flights to foraging grounds and therefore high levels of energy expenditure (Dunn et al., 2020). Although our model was built around data from high-quality individuals (as defined by individuals that survived the annual cycle and had chicks when they were captured), we assume that the times and places that we identified as being potentially vulnerable were likely to be shared by the entire population, including untracked individuals and those that did not survive the annual cycle. Both the periods and places that we highlight as potentially being high risk, due to guillemots being more likely to experience energetic bottlenecks and declines in mass, are supported by ringing recovery data within this region (Wernham et al., 2002). This gives us confidence that our approach is able to successfully identify times and locations where wild animals might experience energetic imbalances, without the need for direct year-round observations (e.g. Lohr et al., 2011; Mann & Watson-Capps, 2005).

Understanding when and where wild animals are at risk of mortality is particularly timely due to global environmental change and

the detrimental impacts that this can have on individual survival and population demography (Jenouvrier, 2013). As well as the impacts of senescence on physiology and behaviour (Elliott et al., 2015), animals are exposed to numerous additional pressures across their annual cycles, including mortality from hunting and poaching (Frair et al., 2007) and competition from fisheries (Karpouzi et al., 2007). Although currently we have not accounted for all sources of mortality, instead focusing on risk of death due to mass losses, additional causes of death (e.g. predation or bycatch mortality associated with fisheries) could be added as extensions to the model in the future if appropriate data become available. This being said, in seabirds, large-scale mortality events outside the breeding season are often associated with severe and prolonged storms which prevent birds from feeding, leading to a negative energy balance, loss of body mass and, ultimately, death (Clairbaux et al., 2021; Harris & Wanless, 1996). Indeed, thermodynamic modelling revealed that high wind speeds elevated the winter energy expenditure of Brünnich's guillemots and little auks *Alle alle*, such that extreme weather conditions were predicted to influence foraging efficiency and energy acquisition, creating an energy bottleneck (Fort et al., 2009). The adult survival rate estimated for the Isle of May population for 2016–2017 (0.87 ± 0.21 standard deviation) was lower than that during the preceding 5-year period (0.93 ± 0.07 standard deviation, Horswill et al., unpubl. data) suggesting that conditions were relatively unfavourable. Although, by definition, all the birds in our study survived the annual cycle, it is plausible that in individuals which did not survive, mass loss continued over longer durations, impairing body function and ultimately resulting in death. Understanding how wild animals, such as guillemots, cope with potential environmental bottlenecks is critical, particularly when extreme temperatures and storms are predicted to become increasingly severe and frequent under global climate change scenarios (Rahmstorf & Coumou, 2011). By expanding our approach, it might therefore become possible to model inter-annual variability in the timing and duration of low masses in relation to the location and severity of extreme environmental conditions. The approach also accommodates improved estimates of time energy budgets from different biologging devices as well as additional data streams than were available in the current study. Furthermore, this approach could be applied to species from other trophic levels and taxonomic groups, thereby allowing the formation of mechanistic links between environmental covariates and inter-annual variability in animal survival.

5 | CONCLUSIONS

The annual cycles of many wild, mobile animals are difficult to observe and so our knowledge of how animals balance their energy budgets throughout the year remains limited, despite its importance for individual survival, reproduction and therefore population dynamics. Using biologging data and conventional methodologies to calculate daily time-activity budgets, locations and estimates of energy expenditure, we were able to develop a hierarchical Bayesian state-space model to estimate the previously hidden components of energy budgets throughout a full annual cycle. Gaining insights into these components of year-round animal energy budgets, namely individual energy gain and storage, allows a far more detailed understanding of when and where individuals, and therefore populations, might both exert energetic pressure (via prey consumption) and experience energetic bottlenecks. The use of biologging data within energetics-based state-space models offers major opportunities to provide novel insights into the energy balances and even potential susceptibility to mortality of other wild, mobile animals.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

S.W., M.P.H., M.A.N., M.I.B. and F.D. contributed to the planning, collecting and management of the data. R.E.D., J.M. and C.H. analysed the data and R.E.D. led the writing of the manuscript under the supervision of J.A.G., J.M. and S.W. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Environmental Information Data Centre https://doi.org/10.5285/1cc5dcdb-e894-4973-a5b5-7a38a6cfc770 (Dunn et al., 2022).

ORCID

Ruth E. Dunn https://orcid.org/0000-0003-0927-2734
Jonathan A. Green https://orcid.org/0000-0001-8692-0163
Catharine Horswill https://orcid.org/0000-0002-1795-0753
Francis Daunt https://orcid.org/0000-0003-4638-3388
Jason Matthiopoulos https://orcid.org/0000-0003-3639-8172

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