Research article

Energetic synchrony throughout the non-breeding season in common guillemots from four colonies

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The non-breeding season presents significant energetic challenges to birds that breed in temperate or polar regions, with clear implications for population dynamics. In seabirds, the environmental conditions at non-breeding sites drive food availability and the energetic cost of regulatory processes, resulting in variation in diet, behaviour and energetics; however, very few studies have attempted to understand if and how these aspects vary between populations. We investigated whether non-breeding location influenced diet, behaviour and energetics in the common guillemot *Uria aalge*. We studied guillemots from four UK breeding colonies, two located on the west coast of Scotland and two on the east. We quantified non-breeding distribution, foraging behaviour and activity budgets of 39 individuals from July to March, using geolocation–immersion loggers and time-depth recorders, and used feather stable isotope signatures to infer diet during the post-breeding moult. We calculated energy expenditure and investigated whether the peak (an indicator of the potential vulnerability to marine threats) varied between colonies. Individuals were spatially segregated according to the coastline they breed on, with west coast guillemots distributed off the west coast of the UK and east coast guillemots distributed off the east coast. Diet and behaviour were more similar in guillemots that shared a breeding coastline than those that did not, as west coast guillemots foraged at a lower trophic level, spent less time diving and engaged in more pelagic foraging than east coast guillemots. However, energy expenditure was remarkably similar between colonies, peaking during late February/early March, indicating that, during our study period, there was high synchrony between colonies in the timing of potential vulnerability to marine threats. Therefore,

any anthropogenic changes that result in decreased food availability or increased energy expenditure during late winter may have greater impacts on energy balance, with consequences for population dynamics.

Introduction

The non-breeding season presents significant energetic challenges to long-lived birds that breed in temperate or polar regions. The environmental conditions experienced during the non-breeding season and their energetic consequences underpin an individual's likelihood of surviving to the following breeding season (Andreev 1999) and therefore have important implications for population dynamics. The energetic challenges of the non-breeding season can be compounded by interaction with anthropogenic threats with energetic consequences, such as by impeding foraging ability or increasing energetic costs of processes such as thermoregulation or migration (Tomlinson et al. 2014). However, despite the important link between non-breeding season energetics and population dynamics, this topic has been understudied within avian ecology. Recent advancement of techniques such as biologging and diet biomarkers have allowed us greater understanding of year-round diet, foraging behaviour and activity budgets (Crossin et al. 2014), all factors that may impact energetics during the non-breeding season. Seabirds have historically been difficult to monitor during the non-breeding season, yet they are required to return to land to breed, thus the breeding season provides an opportunity for biologging and tissue sampling. These methodological advances have led to an explosion of studies over the last two decades on non-breeding diet (Wiley et al. 2019), foraging behaviour (Goetz et al. 2018) and activity budgets (Harris et al. 2020) in seabirds.

Despite this recent expansion of studies, only a handful have investigated seabird energetics during the non-breeding season (Green et al. 2009, Fayet et al. 2017, Amélineau et al. 2018, Dunn et al. 2019, 2020, Clairbaux et al. 2021) and none have incorporated diet, foraging behaviour, activity budgets and energy expenditure to gain a comprehensive view of non-breeding ecology and energetics. Understanding these processes collectively is important because seabirds are exposed to harsh environmental conditions during the non-breeding season, with lower food availability (Osborn et al. 1984), constrained ability to gain energy through foraging, due to extreme weather events (Morley et al. 2016, Clairbaux et al. 2021) and fewer daylight hours (Daunt et al. 2006), and increased energetic costs of processes such as thermoregulation (Croll and McLaren 1993, Fort et al. 2013). In addition, seabirds may undergo life-history events during the non-breeding season, such as feather moult, which is energetically-expensive (Green et al. 2004) and can result in flightlessness and thus reduced mobility in some species (Bridge 2006). Accordingly, many species of seabird experience their highest levels of mortality during winter (Harris et al. 2007, Acker et al. 2021). Furthermore, seabirds are exposed to a wide range of marine threats throughout the annual cycle, such as hunting, oil spills, marine renewable development, fisheries bycatch and harvesting (Dias et al. 2019). Such threats may cause direct mortality, or may have more indirect negative consequences for diet, behaviour and energetics (Masden et al. 2010) and thus could ultimately lead to reduced survival in individuals that are already at or near sustainable limits to their energy expenditure (Halsey et al. 2018). Understanding the potential impacts of anthropogenic changes that may cause disturbance or displacement, such as marine renewable development (Searle et al. 2014), requires improved knowledge of seabird energy budgets and the locations and timings of potential energetic bottlenecks (where supply of energy does not meet demand).

As non-breeding location has been linked to the likelihood of surviving the winter (Reynolds et al. 2011, Grémillet et al. 2020), it is likely that the environmental conditions experienced during the non-breeding season drive the diet, foraging behaviour, activity budgets, and consequent energetics of individuals. Non-breeding location is also linked to the location of the breeding colony (Tavecchia et al. 2008, Genovart et al. 2018), thus energy expenditure during the non-breeding season may result in different population trends between breeding populations. As protected areas and other conservation measures are generally breeding population-specific in seabirds, it is important to quantify why trends may vary between colonies in order to ensure all are being adequately protected throughout the annual cycle. Despite the importance of understanding population-level differences, only one study to date has investigated non-breeding season energetics in seabirds across multiple breeding colonies. Fayet et al. (2017) found considerable variation in behaviour and energy expenditure between individuals from different breeding colonies and consequences for subsequent reproductive success in the Atlantic puffin *Fratercula arctica*. However, the large spatial scale of Fayet et al. (2017) meant that biogeographical effects and human impacts at the regional scale are likely to have been factors in the patterns observed (Anderson and Jetz 2005, Dunn et al. 2018). Previous studies during the breeding season have highlighted population-level variation in diet and behaviour due to fine-scale variation in environmental conditions (Anderson et al. 2014, Trevail et al. 2019), with consequences for population dynamics. There is therefore a clear need to understand how variation on a smaller scale may impact non-breeding season diet, behaviour and energetics in seabirds, in order to assess population-level vulnerability to anthropogenic changes that may impact non-breeding season energetics (Furness et al. 2013).

In this study, we investigate whether breeding colony influences non-breeding distribution, diet, foraging behaviour, activity budgets and energy expenditure in common

guillemots *Uria aalge* (hereafter 'guillemots'). Previous single-colony studies of guillemots have found temporal variation in foraging behaviour and energetics throughout the non-breeding season (Fort et al. 2013, Dunn et al. 2020), and, using stable isotope analysis, observed high levels of individual variation in their non-breeding season foraging niche (St John Glew et al. 2018). Marine threats can have significant impacts on guillemot activity budgets and energetics; for example, competition with fisheries may lead to localised food shortages (Vader et al. 1989) and marine renewable energy devices may both displace individuals from preferred foraging habitat and increase flight time (Furness et al. 2013, Searle et al. 2014, Peschko et al. 2020). As guillemots have one of the highest wing-loadings of any volant bird species, flight is an extremely expensive behaviour, so marine threats that increase flight time can disproportionately affect energetics (Elliott et al. 2013, Schraft et al. 2019). We studied guillemots from four UK breeding colonies, with two located on the west coast of Scotland and two on the east (Supporting information). Guillemots that breed on the same UK coastline are likely to have more similar non-breeding distributions, as they typically remain distributed in waters on the same side of the UK that they breed on throughout the annual cycle (Buckingham et al. 2022a). However, there are fine-scale environmental differences between the west and east coasts of the UK; for example, environmental heterogeneity is generally greater off the west coast of the UK than the east coast (Trevail et al. 2019), water depth is slightly higher off the west coast of the UK (Supporting information), and there is variation in temporal patterns of sea surface temperature between the coasts, with waters off the west coast of the UK typically cooler during late summer, but warmer during mid-winter (Supporting information). The scale of our study therefore allowed us to investigate the behavioural and energetic consequences of this relatively fine-scale environmental variation. We predicted that there would be less variation in non-breeding season distribution, diet, behaviour and energy expenditure in guillemots from colonies that shared a coastline than in guillemots from colonies located on different coastlines and asked four questions: 1) do guillemots that breed on the same coastline have a more similar non-breeding distribution?; 2) are post-breeding moult diet, foraging behaviour, activity budgets and overall energy expenditure

also more similar in guillemots from the same coastline, in line with non-breeding distributions?; 3) are any differences in seasonal patterns in energetics between guillemots from different colonies driven by behavioural differences or non-breeding distribution?; and 4) are there periods of the non-breeding season when there is increased population-level vulnerability of guillemots to marine threats, based on their behaviour and energy expenditure?

Methods

Data collection

Geolocation–immersion loggers (hereafter 'geolocators'; Biotrack MK3006) and time-depth recorders (hereafter 'TDRs'; Cefas G5 standard) were deployed on 61 breeding adult guillemots during late June and early July 2019 at two west coast (Colonsay and the Treshnish Isles) and two east coast (Whinnyfold and the Isle of May) colonies in Scotland, UK (Supporting information). Geolocators measured light levels, salt water immersion and sea surface temperature (SST). TDRs measured high-resolution temperature and pressure. Through combining these streams of data, we were able to track both location and activity throughout the non-breeding season (approximately mid-July–early March).

Individuals were caught at the breeding site using a noose pole during late incubation or chick rearing. Birds were equipped with a unique metal ring (if not already present), a geolocator mounted on a plastic colour ring on the same leg, and a TDR attached to a second plastic colour ring on the other leg. These deployments were made under licence from the British Trust for Ornithology. Breeding adults were recaptured during June and July 2020 and 2021 using the same capture method, or during attendance at the colony prior to laying (March 2020 and 2021) by use of a mistnet positioned close to the breeding ledge. During device retrieval, the distal two-thirds of a single secondary wing feather was cut for stable isotope analysis (all colonies except Treshnish) under licence from the British Trust for Ornithology or UK Home Office. In all cases, handling times did not exceed ten minutes during either device deployment or retrieval. Total numbers of deployments and retrievals are presented in Table 1.

Table 1. Sample sizes of deployed and retrieved loggers and processed combined datasets; numbers of secondary feathers sampled on device retrieval; and stable isotope datasets retained for analyses. For the latter, individuals were retained if they had combined and processed logger datasets and their core post-breeding moult distribution (31 days from 16 August 2019 to 15 September 2019, inclusive) overlapped with the UK isoscape area by ≥ 95% (Supporting information).

Colony	Loggers				Stable isotopes	
		Retrieved		Combined and processed datasets	Feather samples	Datasets retained after isoscape overlap analysis
	Deployed	TDR	GLS			
Colonsay	15	9	9	8[†]	9	5
Treshnish	15	10	10	10	–	–
Whinnyfold	15	15	12	12	13	11
Isle of May	16	13	12	9[*†]	12	9
Total	61	47	43	39	34	25

*TDR failed early; †GLS failed/failed early.

Although we did not collect data on the sex of individuals, we do not have any reason to believe that the sex ratio of tracked birds was unbalanced within or between colonies.

Device effects

The data loggers and method of attachment chosen were designed to have minimal impact on guillemots, which forage using wing-propelled diving (Geen et al. 2019). The mass of the devices plus colour rings (geolocator: 3.7 g; TDR: 4.5 g) comprised 1.07% of the minimum body mass recorded in breeding adults (765 g; Wagner 1999, Harris et al. 2000), which is consistent with recommendations that logger mass should be as small as possible (Bodey et al. 2018, Geen et al. 2019). The disturbance caused to the individuals through the catching and tagging method seemed short-lived, as it appeared that individuals returned to normal breeding behaviour quickly. We were unable to quantify any effects of carrying the loggers on foraging efficiency and demographic rates such as productivity and survival. However, previous studies undertaken on auk species have shown no difference in resighting rate, body mass or breeding success between individuals tagged with a geolocator and those without (Fort et al. 2012, Baak et al. 2021). In addition, a recent study on breeding Manx shearwaters *Puffinus puffinus*, another volant wing-propelled diver, found no significant difference in foraging efficiency, trip duration or breeding success between untagged individuals and individuals deployed with one leg-mounted device (Gillies et al. 2020).

Data processing

Geolocators recorded continuously and sampled light levels every minute, with the maximum light level recorded every ten minutes. Salt water immersion was sampled every three seconds, with the number of samples that were wet recorded for each ten-minute period. Temperature was sampled at the end of each twenty-minute period during which the device was continuously wet. The TDRs switched on every five days starting on the 1st July 2019 and recorded temperature and pressure every 12 s for 24 h until device failure (median TDR failure date: 16/03/2020; range of fail dates: 11/02/2020–01/04/2020; one device that failed on the 26/07/2019 has been excluded).

Two locations per day were derived from the geolocators using the R package 'probGLS' (Merkel et al. 2016) following the methods from Buckingham et al. (2022a). ProbGLS uses an iterative algorithm to determine the most likely track based on light (with day length used to infer latitude and timing of noon used to infer longitude), salt water immersion and temperature data sampled by the geolocator. This method of combining several data types has been shown to reduce the amount of error associated with geolocation (Phillips et al. 2004, Halpin et al. 2021) and allows us to estimate locations during the equinox (autumn: 23 September 2019; spring: 20 March 2020) and surrounding periods, unlike methods that solely rely on light data. From the locations, timings of day,

night and twilight were calculated using the package 'suncalc' in R (Thieurmel and Elmarhraoui 2019), for use in further analysis. Since our focus was the non-breeding season, the date that an individual left the colony after the breeding season was estimated to be when the daily proportion of time that the geolocator was wet exceeded 50% for at least five days (a conservative estimate based on unpublished GPS data of foraging trip lengths during the breeding season of guillemots tracked from the Isle of May). For each individual, the dataset was filtered to only include the first day after they left the breeding colony until TDR device failure (Results).

TDRs were processed using an adjusted script from Duckworth et al. (2020, 2021) to determine dive events, identify and remove errors (e.g. spikes in pressure caused by preening activities) and account for any baseline drift in depth over time, which is a common issue with TDRs. In order to identify depths that were the result of unrealistic maximum rates of change in depth, we calculated the change in depth an individual would be able to achieve during 12 s, our sampling rate. We used the mean rate of descent ($1.38 ms^{-1}$) from Thaxter et al. (2010) plus three standard deviations (SD: $0.16 ms^{-1}$) in order to account for 99% of the error observed and combined this with our sampling rate, resulting in a maximum depth change of 22.32 m within 12 s. Any depth records that exceeded this speed threshold were removed along with any records that exceeded the maximum measuring potential of the TDRs (200 m). All remaining records with a depth greater than 1 m were defined as diving (Duckworth et al. 2020, 2021, Dunn et al. 2020). Individual dives were characterised as excursions of depth greater than 1m and subsequent return to the surface.

Spatial distribution

To determine the core distribution of adults from each colony throughout the non-breeding season, we calculated 50% kernel density contours for all individuals from each colony during each month of the non-breeding season between leaving the breeding colony and device failure (July 2019–March 2020). Kernels were calculated using the functions 'kernelUD' and 'getverticeshr' in the R package 'adehabitatHR', using bivariate normal kernels, ad-hoc smoothing ('href') and a grid cell size of 100 km^2 (Calenge 2006).

Diet

Within marine systems, $\delta^{15}N$ increases at higher trophic levels (Kelly 2000). $\delta^{15}N$ can be extracted from various body tissues, including feathers, thus providing us with valuable data on the diet of an individual when those feathers were grown. Guillemots moult all of their flight feathers (primary and secondary feathers) during the post-breeding moult, which was defined as 31 days from 16 August 2019 to 15 September 2019, inclusive, as the majority of individuals were expected to be undertaking flight feather moult at this time (Birkhead and Taylor 1977, Harris and Wanless 1990). Unfortunately, we were unable to identify individual moult

periods from behavioural data as individuals undertook relatively few flights throughout the autumn, thus we could not definitively say when an individual was unable to fly. $\delta^{15}N$ is spatially variable in UK waters, as shown by the UK isoscape, which describes the basal values of $\delta^{15}N$ calculated using several species of jellyfish, a low trophic level species (St. John Glew et al. 2019). Therefore, in order to determine the relative trophic level individuals foraged at during the post-breeding moult, we calculated the difference between $\delta^{15}N$ of an individual's secondary feather sample, and $\delta^{15}N$ of the UK isoscape within the region an individual was located during this period (St John Glew et al. 2018). The methods outlined above provided a useful comparative measure between colonies, with a greater difference between baseline values and feather samples of one colony would indicating the guillemots from that colony foraged at a higher trophic level than others during the post-breeding moult.

Feathers were stored in paper envelopes in a −20°C freezer post-retrieval for six months prior to $\delta^{15}N$ analysis, which was carried out by Elemtex Ltd (Cornwall, UK). Samples were washed 3 times in a solution of 2:1 chloroform and methanol and rinsed in distilled water, before being oven-dried at 60°C. Subsequently, the samples were run on an ANCA/2020 isotope ratio mass spectrometer, which was set to run in continuous flow mode. Finally, data were normalised using USGS40 and USGS41A, with typical precisions being better than 0.3‰.

In order to calculate the difference between an individual's baseline value of $\delta^{15}N$ and its feather sample value, 50% kernel density contours were calculated (using the same methods described for calculating each colony's monthly core distribution, above) for each individual during their post-breeding moult. Following this, using the UK isoscape of mean $\delta^{15}N$ values available from St. John Glew (2019; Supporting information) the proportion of each individual's core post-breeding moult distribution that overlapped with this UK isoscape was calculated. Individuals were excluded where the area of overlap between the post-breeding moult distribution and the outer boundary of the UK isoscape was less than 95% (3 from Colonsay and 1 from Whinnyfold; Supporting information). Individuals that overlapped with areas of land within the boundary of the UK isoscape were retained, as such individuals were likely to be distributed coastally in locations for which we did have $\delta^{15}N$ isoscape data. For all individuals where we had TDR, geolocator and $\delta^{15}N$ data, and that overlapped sufficiently with the UK isoscape (Table 1), each individual's 50% kernel density contours were overlaid with the UK isoscape and extracted the mean isoscape $\delta^{15}N$ values from within their core distribution. The difference between the mean $\delta^{15}N$ found within an individual's core distribution and the $\delta^{15}N$ value in their feathers ($\Delta\delta^{15}N$) was then calculated.

Foraging behaviour

Dives were categorised into foraging bouts, where more than two dives occurred with less than 180 s of surface time between them (Tremblay and Cherel 2000). To determine whether individuals were generally using a benthic or pelagic (mid-water) foraging strategy, we calculated the proportion of dives that were within the intra-depth zone (IDZ; Tremblay and Cherel 2000, Duckworth et al. 2021). Higher proportions of dives within the IDZ indicate that a more benthic foraging strategy is being used, as dives are likely to have more similar depths when an individual is foraging benthically (Tremblay and Cherel 2000). To calculate the proportion of dives within the IDZ, firstly we determined the maximum depth of each dive (defined above) and calculated the difference between the maximum depths of sequential dives within each foraging bout (Tremblay and Cherel 2000). Subsequently, we calculated the number of dives that had a maximum depth within 10% of the maximum depth of the previous dive and divided this by the total number of dives within the foraging bout minus one (Tremblay and Cherel 2000). Given our relatively low sampling rate (12 s), it is likely that the maximum depth of some dives was missed, making our analysis hard to compare directly to other studies (Tremblay and Cherel 2000). However, foraging bouts with a higher proportion of IDZ dives will contain a greater proportion of benthic dives and we believe that this metric provides a useful comparative index of change in foraging behaviour over time and between colonies.

Behaviour allocation and daily energy expenditure

To classify different behaviours, the processed TDR and geolocator data were combined using a bespoke procedure based on previous similar studies (Fayet et al. 2017, Dunn et al. 2020, Duckworth et al. 2021). As the TDR and geolocator data were at different temporal scales, we assigned each 12 s TDR measure to a ten-minute wet-dry period and a twice-daily location (noon and midnight). We then calculated daily mean sea surface temperature (SST) from either the geolocator (which only recorded when submerged in salt water) or from the TDR (which recorded continuously) during dive events when geolocator temperatures were not available. Geolocators were used in preference as they could only measure temperature values of salt water, thus we judged these measures to be more reliable than those from TDR dive events, where the method of continuous temperature recording in the TDR may involve a lag from previous activities. Using these settings, for each day of TDR recording, we assigned each 12 s measure to time spent in five behaviours: diving (T_{Dive}), inactive on water ($T_{Inactive}$), active on water (swimming, preening and otherwise alert on the water's surface; T_{Active}), flight (T_{Flight}) and colony attendance (T_{Colony}). Full details of the behavioural allocation methods are in the Supporting information.

Subsequently, we filtered the data to remove incomplete days (0.81% days) and calculated the duration of time spent in each behaviour for each day. Daily energy expenditure (DEE) was then calculated for each day of TDR recording using the following equation (Elliott et al. 2013, Elliott and

Gaston 2014, Burke and Montevecchi 2018, Dunn et al. 2020, Patterson et al. 2022):

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

where T_{Inactive}, T_{Active}, T_{Flight} and T_{Colony} were measured in hours and T_{Dive} in minutes and SST was the daily mean as described above.

In order to address our third question and elucidate the relative contributions to DEE from temporal changes in SST and behaviour, we created a second set of DEE estimates using a constant value of SST throughout the non-breeding season (15°C). We compared patterns of DEE over time and the contributions of each behaviour to DEE using both observed SST values and with constant SST.

Statistical analysis

For all analyses, we only included individuals that had both TDR and geolocator data (Table 1).

For analyses on stable isotope data, we used linear models using the 'lm' function in R, with $\Delta\delta^{15}$N as a response variable and breeding colony as a fixed effect. We compared the model with colony to a null model using Akaike information criterion (AIC) and selected the model with the fewest parameters within $\Delta2$ AIC of the lowest AIC (Arnold 2010). Subsequently, we used the 'emmeans' package to calculate Tukey pairwise comparisons between colonies.

For analyses on IDZ dives, activity budgets and DEE, we filtered data to ensure that there were at least five individuals per day for each colony. If a colony had fewer than five individuals, we excluded that colony for that day, but retained colonies with sample sizes greater than five in a compromise between sample size and temporal extent of the dataset. We performed generalised additive mixed models (GAMMs) of each response variable against a smooth of day since 1 July, breeding colony, and an interaction term as fixed effects, along with individual ID as a random effect. For analyses on activity budgets and DEE, we used the 'gamm4' package in R, with daily time allocation to each behaviour (diving, active on water, inactive on water, flight and colony attendance) and DEE as response variables. For the analysis of T_{Dive}, T_{Active} and T_{Inactive}, we used models with a logit-normal distribution, with the number of minutes spent in each activity per individual as a proportion of the total minutes available per day as the response variable. As there were a large proportion of zeros for flight and colony attendance behaviours, we converted T_{Flight} and T_{Colony} to presence/absence of flight or colony attendance per individual per day and fitted models with binomial distribution. For the analysis of DEE, we used a Gaussian distribution, with the log-transformed number of joules spent per individual per day

as the response variable. For analysis on IDZ dives, we used the 'mgcv' package, as mgcv allows use of a negative binomial distribution, and set the proportion of dives in each foraging bout that were within the IDZ as the response variable. We compared AIC values of models with gradually reducing numbers of fixed effects 1) temporal smooth, breeding colony and interaction; 2) temporal smooth and breeding colony; 3) temporal smooth only; and 4) breeding colony only) and against a null model (random effect only). We selected the model containing the fewest parameters that was within $\Delta2$ AIC of the lowest AIC (Arnold 2010). We performed model validations of the most parsimonious model by plotting the residuals against the fitted values and model covariates.

All data processing and analysis took place in R ver. 4.0.5 (www.r-project.org).

Results

During March and June–July 2020 and 2021, 43 individuals were recaptured with both TDR and geolocator intact, plus four individuals with TDR only, which lost their geolocator prior to retrieval (Table 1). TDR devices had all run out of battery prior to the 2020 breeding season (as expected) and were returned to the manufacturer for data extraction. Of these, one TDR (from an individual that bred at the Isle of May) appeared to have suffered damage during the early non-breeding season and failed to record data after 26 Jul 2019. In addition, one geolocator (from the Isle of May) failed to record data completely, and two others failed early in the non-breeding season (one from Colonsay 27 Jul 2019 and one from the Isle of May 12 Sep 2019). We excluded all individuals with an early failure date in one or both of their devices from further analyses, which resulted in a final sample size of 39 combined datasets (Table 1). Across all individuals, the median date of leaving the colony, as calculated from the geolocator activity data, was 12 Jul 2019 (range: 30 Jun 2019–24 Jul 2019). The median date of device failure (when either device first failed) from the final sample was 16 Mar 2020 (range: 8 Feb 2020–1 Apr 2020).

Spatial distribution

Non-breeding season distributions were more similar in guillemots that bred on the same coastline than those that did not (Fig. 1). Distributions varied through the non-breeding season, but throughout, the core distributions of guillemots breeding at west coast colonies, Colonsay and Treshnish, were located off the west coast of the UK, whereas the core distributions of guillemots breeding at east coast colonies, Whinnyfold and the Isle of May, were consistently located off the east coast of the UK.

Diet

The most parsimonious model for the difference between δ^{15}N of each individual's secondary feather and the mean
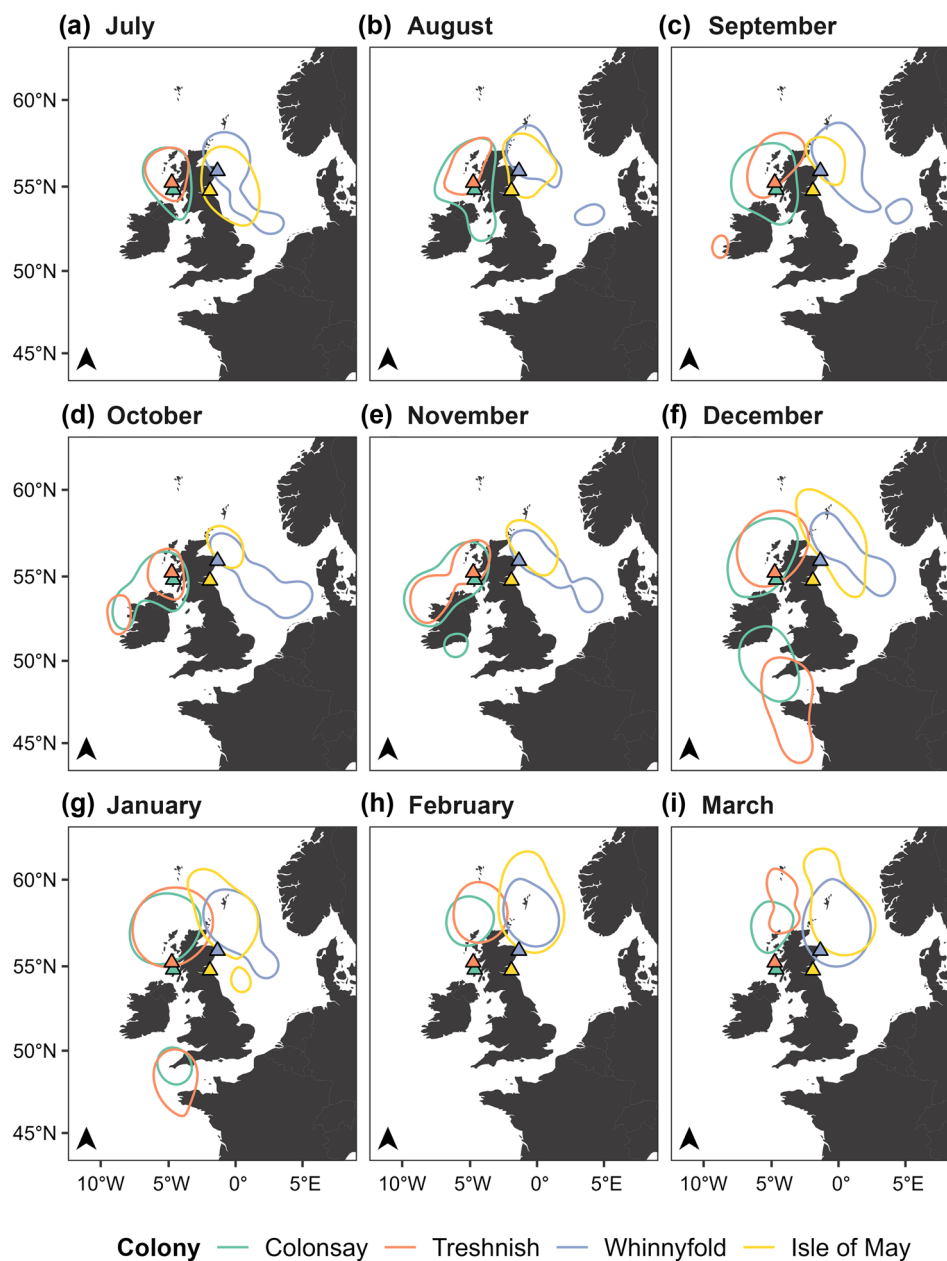
Figure 1. Monthly core areas (50% kernel density contours) for our tracked sample of common guillemots for each breeding colony during July 2019–March 2020.

values extracted from individual 50% kernel density contours during the post-breeding moult ($\Delta\delta^{15}N$) included colony only as a fixed effect (Fig. 2; Supporting information). At both the Isle of May ($p = 0.002$, $df = 20$) and Whinnyfold ($p < 0.001$, $df = 20$), $\Delta\delta^{15}N$ was significantly greater than at Colonsay, but there was no evidence for a difference in $\Delta\delta^{15}N$ between Whinnyfold and the Isle of May ($p = 0.251$, $df = 20$), indicating that individual guillemots that bred at Colonsay fed at a lower trophic level during post-breeding moult than individuals breeding at either Whinnyfold or the Isle of May.

Foraging behaviour

The most parsimonious model for the proportion of dives in each foraging bout that were within the IDZ included a temporal smooth, breeding colony and their interaction term (Fig. 3; Supporting information). The proportion of IDZ dives was relatively low for all colonies early in the non-breeding season and during the post-breeding moult (mid-August– mid-September), with the mean of the smooths ranging from 0.25 to 0.35. Such proportions indicate that guillemots were more likely to be undertaking pelagic dives at this time.
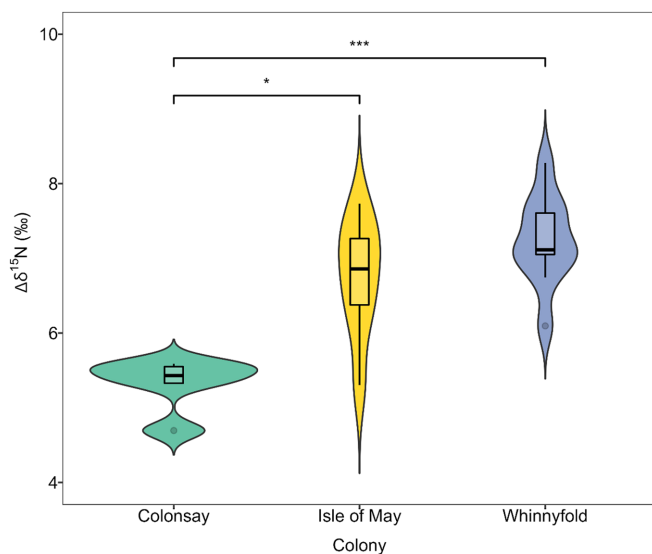
Figure 2. Violin plots showing the difference between δ^{15}N of each individual common guillemot's secondary feather and the mean values of basal δ^{15}N extracted from the UK isoscape for individual 50% kernel density contours during the post-breeding moult ($\Delta\delta^{15}$N), presented by colony. Colonsay is located on the west coast of the UK and the Isle of May and Whinnyfold are located on the east coast. Individuals were retained if they had combined and processed logger datasets and where their core post-breeding moult distribution overlapped with the UK isoscape area by $\geq$ 95% (Supporting information). Post-breeding moult was defined as 31 days from 16 August 2019 to 15 September 2019 inclusive. Significant differences between colonies are marked by bars and asterisks, where * indicates $p < 0.05$ and *** indicates $p < 0.001$.

Subsequently, the proportion of IDZ dives increased to around 0.6 during October for individuals that bred at east coast colonies (Whinnyfold and the Isle of May), indicating a switch towards a more mixed foraging strategy, including both pelagic and benthic dives. Individuals that bred at east coast colonies maintained a significantly higher proportion of IDZ dives than those from west coast colonies (Colonsay and Treshnish) until mid-December, indicating that guillemots from east coast colonies were foraging with a more benthic strategy than those from west coast colonies during autumn and early winter. From December, the proportion of IDZ dives increased at west coast colonies to around 0.6, and individuals from all colonies remained at this level for the remainder of the season, thus indicating that all colonies were undertaking a mixed foraging strategy during the second half of the non-breeding season, with more benthic diving than during the first half of the non-breeding season.

Activity budgets

For time spent diving T_{Dive}, the most parsimonious model included temporal smooth, breeding colony and their interaction term (Fig. 4a; Supporting information). For time spent active on water T_{Active} and inactive on water $T_{Inactive}$, the most parsimonious model included temporal smooth only (Fig. 4b; Supporting information). For presence/

absence of colony attendance, the most parsimonious model included temporal smooth and breeding colony, and for presence/absence of flight the most parsimonious model included a temporal smooth only (Fig. 4c and d; Supporting information).

During July, individuals spent between 2.2 and 4.0 h diving per day and this pattern was fairly consistent between colonies (GAMM predictions on 11 July, the first date with sufficient data at all colonies: Colonsay: 2.57 ± 1.7 h; Treshnish: 4.0 ± 1.9 h; Whinnyfold: 3.4 ± 0.9 h; Isle of May: 2.7 ± 0.8 h; Fig. 4a). Subsequently, T_{Dive} decreased for individuals from all colonies, reaching a low point of 1.8–2.5 h during the autumn (GAMM predictions: Colonsay: 1.9 ± 0.3 h, 21 October; Treshnish: 1.7 ± 0.3 h, 31 August; Whinnyfold: 2.3 ± 0.3 h, 31 August; Isle of May 2.0 ± 0.3 h, 5 September). From early October to December, individuals from east coast colonies spent significantly more time diving than individuals from west coast colonies, a difference that remained until December. Following this point, individuals from different colonies showed diverging temporal patterns in T_{Dive} and peaked at varying times based on our GAMM predictions (Colonsay: 4.3 ± 0.6 h, 31 December; Treshnish: 4.5 ± 1.2 h, 17 March; Whinnyfold: 4.0 ± 0.5 h, 15 January; Isle of May: 5.3 ± 2.0 h, 17 March; Fig. 4a).

Time spent active on water fluctuated throughout the non-breeding season, but there was a general trend of increasing T_{Active} over time, with peak T_{Active} occurring during late February (GAMM predictions: 13.1 ± 0.8 h, 25th February; Fig. 4). Conversely, $T_{Inactive}$ showed a general decreasing trend through the season, with seasonal patterns broadly mirroring those of T_{Active} (Fig. 4b).

Immediately after leaving the breeding colony, around 31% of individual guillemots undertook at least one flight per day (GAMM predictions: $30.7 \pm 24.1\%$; 11 July; Fig. 4c). However, flights rapidly became less common, with fewer than 1% of individuals undertaking a flight between 25 August and 10 September. Thereafter, flights became more common, peaking with around 35% of individuals flying at least once per day in February (GAMM predictions: $35.3 \pm 7.1\%$; 10 February).

We did not record any colony attendance until the 4 October (Colonsay; Supporting information) and colony attendance remained a relatively uncommon behaviour throughout the non-breeding season. As the most parsimonious model contained no interaction between colony and temporal smooth, the modelled daily likelihood of attendance (equivalent to the proportion of individuals attending the colony) reached a peak on the same day for all colonies, on 10 February (GAMM predictions: Colonsay: $7.7 \pm 7.1\%$; Treshnish: $4.5 \pm 4.9\%$; Whinnyfold: $13.2 \pm 7.5\%$; Isle of May: $4.4 \pm 5.7\%$; Fig. 4d).

Daily energy expenditure

The best performing model for DEE included a temporal smooth, breeding colony and their interaction term (Fig. 5; Supporting information). Based on our GAMM predictions,
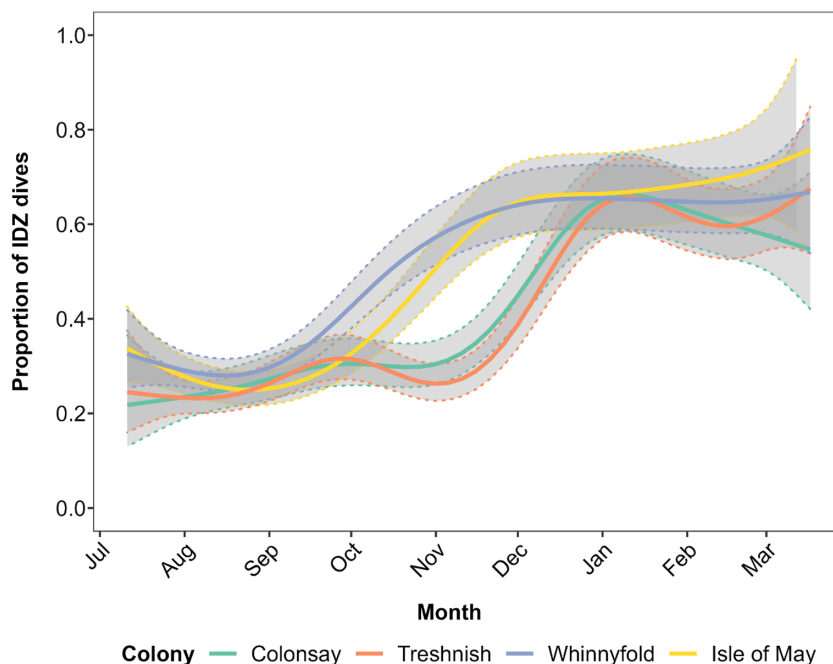
Figure 3. The proportion of dives in each foraging bout (more than two dives within 180 s of each other) per individual common guillemot that were within the intra-depth zone (IDZ; the number of dives within each foraging bout that had a maximum depth of within 10% of the maximum depth of the previous dive divided by the total number of dives within the foraging bout minus one). Higher values indicate a more benthic foraging strategy. Solid lines represent the temporal smooth for each colony, with grey bars and dotted lines representing the area within the upper and lower confidence intervals (two standard errors above and below the mean) extracted from generalised additive mixed models. Colonsay and Treshnish are located on the west coast of the UK and the Isle of May and Whinnyfold are located on the east coast. Raw data are presented in the Supporting information.

DEE was lowest during July/August (Colonsay: 1258 = 9 ± 219 kJ, 11th July; Treshnish: 1378 ± 58 kJ, 25 August; Whinnyfold: 1358 ± 91 kJ, 11 July; Isle of May: 1333 ± 58 kJ, 11 July) and increased throughout the non-breeding season, reaching its highest point during late February/early March (Colonsay: 1889 ± 97 kJ, 20 February; Treshnish: 2041 ± 126 kJ, 17 March; Whinnyfold: 1929 ± 92 kJ, 6 March; Isle of May: 1976 ± 87 kJ, 17 March). Although we observed significant differences between the different colonies in smooth shape and intercept, there was no substantial difference in patterns of DEE over time between colonies, with guillemots from all colonies' DEE peaking and dipping at similar points during the non-breeding season (Fig. 5).

To investigate whether there were significant differences between colonies across the non-breeding season as a whole, we summed and plotted the mean and 95% confidence intervals of our GAMM predictions. Based on comparison of means and confidence intervals, there were no significant differences between-colonies in summed energy expenditure across the non-breeding season (Supporting information).

When DEE was modelled using a constant value of SST (15°C), DEE still increased through the non-breeding season, but at a much slower rate than when using observed SST values (Supporting information). In addition, flights contributed much more to DEE later in the year (Supporting information). Peak values of DEE occurred during late February/early March under both models, which indicates

that the increase in DEE that we observed was driven primarily by decreasing SST, but was increased in magnitude by behavioural changes.

Discussion

Here, we investigated distribution, post-breeding moult diet, foraging behaviour, activity budgets and DEE in guillemots from four UK breeding colonies during the non-breeding season. Despite the relative close proximity of the breeding colonies, we observed inter-colony variation in distribution, diet, foraging behaviour and activity budgets. Non-breeding distribution, diet and foraging behaviour were more similar in guillemots that bred on the same coastline of Scotland (east or west) than those that did not. However, guillemots from all colonies had remarkably similar temporal patterns and magnitudes of DEE, which is relevant for assessing their potential vulnerability to anthropogenic changes.

We found relatively low differences in DEE between colonies, in contrast to Fayet et al. (2017), which is likely due to the smaller geographical range of our study. Fayet et al. (2017) sampled colonies across the entire breeding range of the Atlantic puffin, whereas we investigated variation between guillemot colonies that were less widely distributed. While the guillemots in our study stayed primarily in waters on the UK continental shelf, they likely experienced local variation in key
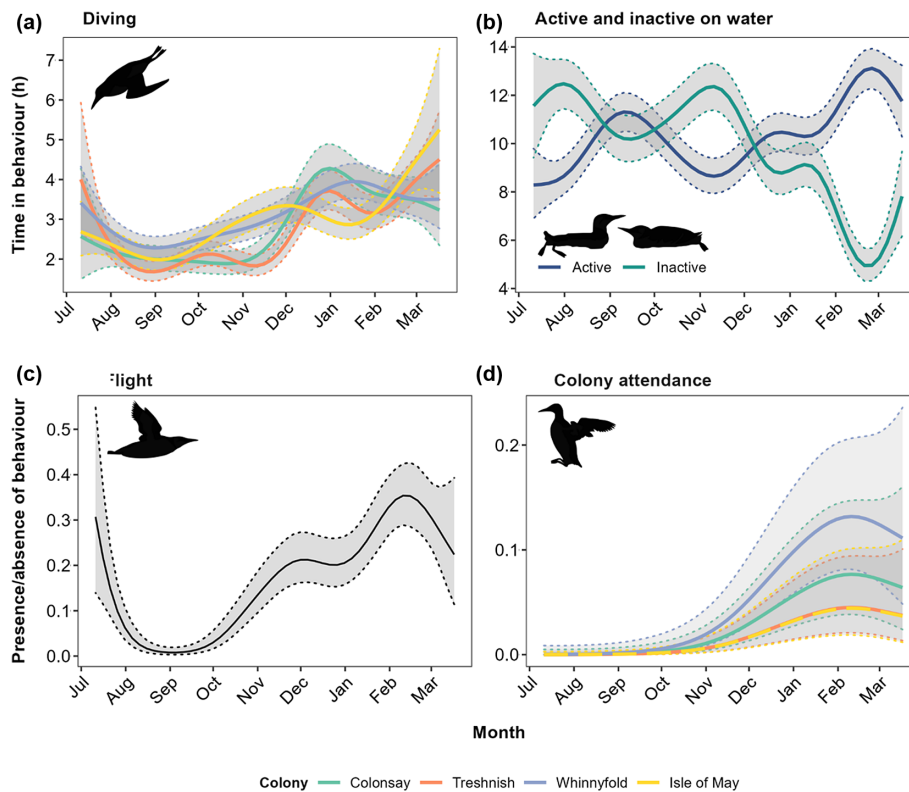
Figure 4. Time spent (a) diving and (b) active and inactive on water; and presence (1) and absence (0) of (c) flight and (d) colony attendance per individual common guillemot per day. Solid lines represent the temporal smooth of the best fitting model, with colony effects observed for time diving (a) and colony attendance (d). Grey error bars and dotted lines representing the area within the upper and lower confidence intervals (two standard errors above and below the mean) extracted from generalised additive mixed models. Due to the high overlap in smooth between Treshnish and the Isle of May in (d), the Isle of May is shown as a dashed line to enable visibility of both colonies. Colonsay and Treshnish are located on the west coast of the UK and the Isle of May and Whinnyfold are located on the east coast. Raw data are presented in the Supporting information.

environmental conditions, such as bathymetry (Supporting information) and SST (Supporting information), but the high similarity in DEE between populations suggested that the energetic consequences of this environmental variation were relatively small. Our study therefore reinforces previous findings that guillemots adjust their behaviour to their environmental conditions to manage their energy expenditure (Dunn et al. 2020). Behavioural and dietary flexibility in response to environmental conditions has previously been observed in auks (Reed et al. 2006, Fort et al. 2013, Shoji et al. 2014, St John Glew et al. 2019, Dunn et al. 2020) and other seabird species (Green et al. 2005, Quillfeldt et al. 2010, van Bemmelen et al. 2017, Bourgeois et al. 2022) and is an important predictor of a species' ability to adapt to anthropogenic change (Snell-Rood 2013). Species that show greater behavioural and/or dietary flexibility are typically more able to adapt to anthropogenic pressures that cause disturbance or reduced habitat, as they are more able to switch to alternative foraging strategies or move to new locations (Snell-Rood 2013). In addition, as our values for DEE were relatively low compared to other guillemot populations determined using a similar approach (Burke and Montevecchi 2018), it is likely that none of our study populations were under immediate

energetic stress. However, the peak of DEE during late winter/early spring indicates that this is a period of increased vulnerability, during which guillemots may be more vulnerable to threats that either increase their energy expenditure or decrease their energy intake.

The temporal patterns of DEE that we observed were similar to those recorded in a previous study of guillemot energetics during the non-breeding season (Dunn et al. 2020), which focussed on individuals that bred at the Isle of May during the 2005–2006 non-breeding season. In both our study and Dunn et al. (2020), peak DEE occurred during the harsh environmental conditions of late winter and the lead-up to the breeding season. However, our DEE estimates were lower than those in Dunn et al. (2020), which highlighted a peak in predicted DEE of 2212 kJ during April, 11.2% greater than our peak of 1976 kJ for the Isle of May during mid-March. These differences in DEE between our study and Dunn et al. (2020) may either be the result of using different biologging devices and consequent small methodological differences for estimating activity budgets, and/or differences in environmental conditions between study years (Johns et al. 2020). As the temporal variation in DEE that we observed was driven primarily by variation in
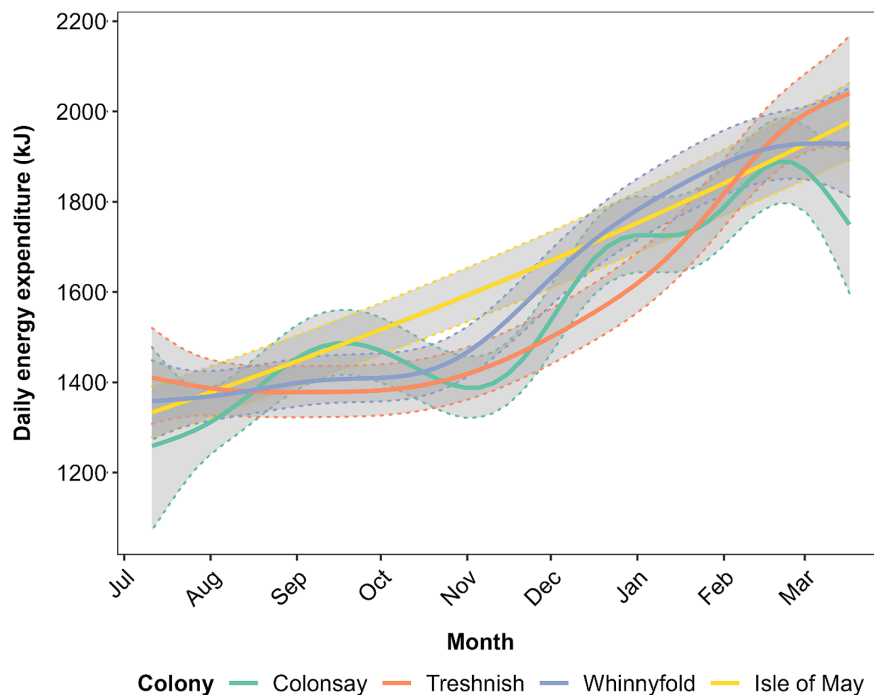
Figure 5. Daily energy expenditure per individual common guillemot per day. Solid lines represent the temporal smooth for each colony, with grey bars and dotted lines representing the area within the upper and lower confidence intervals (two standard errors above and below the mean) extracted from generalised additive mixed models. Colonsay and Treshnish are located on the west coast of the UK and the Isle of May and Whinnyfold are located on the east coast. Raw data are presented in the Supporting information.

SST and, to a lesser extent, by altered behavioural budgets, it is likely that environmental conditions are a key driver of DEE variation between years. Indeed, we observed higher values of SST during late winter compared with Dunn et al. (2020; Supporting information), indicating that guillemots experienced less harsh winter conditions with respect to temperature during our study than during Dunn et al.'s (2020). As our study focussed on breeding colonies that experience a relatively temperate climate throughout the annual cycle, it is also likely that the non-breeding conditions within this study were less harsh than those experienced by other colonies in the northern part of the species range. Correspondingly, our temporal patterns of DEE were different to those observed in guillemots that breed in the north-west Atlantic, where DEE was consistently high between December and late February (Fort et al. 2009, Burke and Montevecchi 2018). This is most likely due to the lower SSTs in the north-west Atlantic during the non-breeding season, again indicating the critical influence of temperature on DEE. Such high energetic output is likely sustained due to the increased availability of high quality food (Frederiksen et al. 2016).

During our study, we observed a decrease of SST during the non-breeding season (Supporting information), which increased the energetic cost of guillemots being both active and inactive on water. In addition, as the non-breeding season progressed, guillemots from all colonies spent increasing time in more energetically-costly activities, such as flight, foraging and active on water behaviours, with less time spent resting on the water. The increase in time active

on water was likely in part a consequence of increased time diving, as behaviours undertaken within active on water include pauses between dives. In addition, as the non-breeding season progressed and guillemots spent increasing time flying, less time would have been available for resting on the water. It is unlikely that these behavioural changes were driven by changing day length as, for example, there was relatively low time spent diving and few flight occurrences during September, but relatively high time spent diving and more flight occurrences during March, despite both periods having similar amounts of day and night time. SST was significantly lower for east coast guillemots during mid-November to mid-February (Supporting information), which increased the costs of both active and inactive on water for east coast guillemots compared to west coast guillemots during this period. During October–December, we observed behavioural differences between coastlines, with east coast guillemots spending more time diving than west coast guillemots (Fig. 4a). Guillemots are highly adapted to diving, with one of the highest wing-loadings of any volant bird species, thus diving is a relatively low-cost activity (Elliott et al. 2013). Correspondingly, we observed relatively low contributions to DEE from diving activity throughout the season (Supporting information). As we observed no clear difference in DEE between west and east coast guillemots during the period of substantially different SST (mid-November–mid-February), it is likely that the increased costs of active and inactive on water behaviours for east coast guillemots during this time are balanced by

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increased time spent diving, when energy is saved via thermal substitution (Kaseloo and Lovvorn 2006).

During our study period, guillemots that bred on the west coast of Scotland foraged at a lower trophic level during the post-breeding moult than guillemots that bred on the east coast. Though we did not have diet data available for one of our west coast colonies (Treshnish), similarities in location and diving behaviour make it likely that guillemots from Treshnish had a similar post-breeding moult diet to those from Colonsay. Guillemots forage on a wide range of prey during the non-breeding season, including fish species, such as clupeids, gadoids and sandeels, and zooplankton (Blake 1983, Blake et al. 1985, Ouwehand et al. 2004), thus it is likely that the diet of east coast guillemots had higher proportions of fish and relied less on zooplankton than west coast guillemots during the post-breeding moult. Despite differences in diet between west and east coast guillemots, individuals from all colonies exhibited similar foraging strategies during the post-breeding moult, being more likely to undertake pelagic dives during this period. As the non-breeding season progressed, guillemots from all breeding colonies switched their strategy to a mix of benthic and pelagic foraging, with east coast guillemots switching to more benthic diving earlier in the season than west coast guillemots. Foraging strategy appeared to be similar in temporal pattern to time spent diving, with increases in daily dive time mirroring the switch toward more benthic diving; thus east coast guillemots spent more time diving earlier in the season than west coast guillemots. It is likely that the differences that we observed between west and east coast guillemots' diet during the post-breeding moult and foraging strategy is partly driven by the variation between their non-breeding regions in bathymetry, with east coast guillemots distributed through shallower waters than west coast breeders (Supporting information), resulting in more accessible benthic prey. Increased time diving combined with a more benthic foraging strategy may indicate that guillemots from east coast colonies had higher energetic intake in terms of volume and/or quality of prey during autumn and early winter, or that they invested more time diving to gain higher value prey items at a lower success rate.

Marine threats that impact the energetics of guillemots within our study region include extreme weather events, competition with fisheries and displacement effects from renewable energy developments. Extreme weather events, such as winter storms, can cause mass mortality in guillemots and other seabirds (Harris and Wanless 1996), which appears to be driven by an inability to gain energy during extreme weather (Clairbaux et al. 2021). Extreme weather events are predicted to become more common and more severe under most climate change scenarios (IPCC 2018), but as it is extremely difficult to predict how climate change will impact conditions at the local scale, it is unclear whether exposure to extreme weather will change at dramatically different rates between our study populations. Although guillemots are thought to have relatively low vulnerability to competition with fisheries, mostly driven by their high dietary flexibility and diving ability (Furness and Tasker 2000), competition

with fisheries can create localised food shortages for guillemots (Vader et al. 1989). The majority of the UK's landings of pelagic and benthic fish are extracted from the northern North Sea (Marine Management Organisation 2021), which overlaps more closely with the non-breeding distributions of guillemots that breed on the east coast of Scotland, potentially rendering them more vulnerable to this threat. The North Sea and coastal Scottish waters are highlighted for offshore wind farm development (The Scottish Government 2020, The Crown Estate 2021), areas that are used extensively during the non-breeding season by guillemots from all our study colonies. Guillemots can be displaced from offshore wind farms (Peschko et al. 2020), which may prevent them from accessing important foraging habitats (Dierschke et al. 2016) and/or prompt escape behaviours, such as flight (Fliessbach et al. 2019), thus increasing energy expenditure. Overall, exposure and vulnerability to marine threats for guillemots in our study region is currently relatively similar across populations. However, despite the DEE values observed in guillemots during our study year being well within their potential limits, it is possible that the high levels of current or planned anthropogenic activity within our study region may result in reduced food availability or increased energy expenditure for guillemots in the future, which should be considered within impact assessments.

We have developed a novel method for estimating time in activity budgets in common guillemots, which adapted the methods of previous studies of auks (Fayet et al. 2017, Dunn et al. 2020). Elucidating the differences in tag responses between flight or colony attendance and inactive on water, all of which result in a dry geolocator device, is notoriously difficult in species that leg-tuck (Linnebjerg et al. 2014). However, the temporal patterns of flight and colony attendance we estimated are consistent with our knowledge of the ecology of this species, with a clear period of greatly reduced flights during the post-breeding moult and no colony attendance between mid-July and October (Harris and Wanless 1990), which suggests that our classification method is robust. Due to the low number of flight and colony attendance behaviours recorded during the early non-breeding season, we were unable to highlight precise individual or colony-level timings of the post-breeding moult, which would be of great use for highlighting periods of increased vulnerability and for improving our understanding of how the timing of post-breeding moult varies among populations. In addition, we did not account for the cost of feather growth within our DEE equation, but as various moults (post-breeding, body and pre-breeding) occur from July to December (St John Glew et al. 2018), and potentially outwith this period at some colonies, feather growth is likely to present a persistent, yet small, additional cost to DEE throughout the non-breeding season. Overall, we believe that the behavioural model that we present is the best current estimation of activity budgets for guillemots during the non-breeding season, as we had high quality foraging data and were more able to distinguish between flight or colony attendance and leg-tucking compared to previous methods.

Wider implications

We have highlighted a consistent period of high energy expenditure during late winter/early spring in guillemots from four UK breeding colonies, despite fine-scale inter-colony variation in environmental conditions, diet and behaviour. The colonies we studied appear to have similar vulnerability to marine threats that impact their energetics during the non-breeding season, which may be applicable for other populations that are located relatively closely together with fine-scale environmental variation. Vulnerability will therefore depend primarily on the nature, intensity and location of these marine threats. Our study region is facing unprecedented anthropogenic change, the full extent of which is yet to be determined. As a result we do not yet fully understand how this may impact different guillemot populations. We therefore hope that our findings will be used to assess the impacts of such change and the development of similar estimates of vulnerability in other seabird species.

Author contributions

Lila Buckingham: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Writing – original draft (lead). **Francis Daunt**: Conceptualization (equal); Funding acquisition (equal); Supervision (supporting); Writing – review and editing (equal). **Maria Bogdanova**: Conceptualization (equal); Supervision (supporting); Writing – review and editing (equal). **Bob Furness**: Conceptualization (equal); Funding acquisition (equal); Supervision (supporting); Writing – review and editing (equal). **Sophie Bennett**: Data curation (equal); Formal analysis (supporting); Writing – review and editing (supporting). **James Duckworth**: Formal analysis (supporting); Writing – review and editing (supporting). **Ruth Dunn**: Formal analysis (supporting); Writing – review and editing (supporting). **Sarah Wanless**: Data curation (equal); Writing – review and editing (supporting). **Michael Harris**: Data curation (equal); Writing – review and editing (supporting). **David Jardine**: Data curation (equal); Writing – review and editing (supporting). **Mark Newell**: Data curation (equal); Writing – review and editing (supporting). **Robin Ward**: Data curation (equal); Writing – review and editing (supporting). **Ewan Weston**: Data curation (equal); Writing – review and editing (supporting). **Jonathan Green**: Conceptualization (equal); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from Zenodo: https://zenodo.org/record/7327472#.Y7_FOHbMK4s (Buckingham et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

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