Distribution and time budgets limit occupancy of breeding sites in the nonbreeding season in a colonial seabird

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To acquire or retain a higher quality breeding site, individuals may occupy sites outside the breeding season, with those investing more time and energy in this benefiting from improved breeding success. However, despite this benefit, the occupancy patterns of individuals may vary. Occupancy may be influenced by the distance individuals travel from breeding sites during the nonbreeding season; individuals nearer the colony may undertake occupancy earlier and more frequently than conspecifics because of shorter commuting distances from migration and foraging locations. Occupancy may also be energetically costly and affect how individuals are able to allocate their time to other key behaviours such as foraging. However, our understanding of how occupancy behaviour relates to an individual's distribution and ability to balance time and energy allocated to other behaviours is limited. Using data from a population of common guillemots, *Uria aalge*, a colonially breeding seabird, on the Isle of May, U.K., we investigated how nonbreeding occupancy of breeding sites is related to at-sea distribution, and how much energy and time individuals allocate to behaviours throughout the nonbreeding season We used bird-borne geolocators and time-depth recorders to record distribution and estimate time allocated to behaviours including occupancy, flight and foraging. Individuals that remained nearer to the colony before their first return then returned earlier and had shorter bouts of absence thereafter. Individuals also experienced a trade-off in the time spent in occupancy or foraging. Our data allowed us to estimate the increase in foraging efficiency required to offset the lost foraging time in individuals that occupied breeding sites. Overall, despite its known benefits, individuals varied in their timing and pattern of occupancy. We suggest that achieving consistently high breeding success, via nonbreeding season occupancy, may depend on an individual's distribution and ability to forage efficiently throughout the nonbreeding season.

How well individuals cope with the pressures faced in the nonbreeding season will affect their survival probability and potentially carry over to affect future fitness measures such as breeding success. Variation between individuals may be driven by the individual's ability to mitigate the pressures facing them (Rödel et al., 2004). Some individuals may be better able to cope with external stressors, for instance by foraging more efficiently (Guillemain et al., 2013; Illius et al., 1995). Individual qualities may therefore contribute to the variation in the behaviour adopted by individuals at this critical time. One of the best understood relationships between nonbreeding season behaviour and subsequent breeding performance is the timing of return to breeding sites or territories following winter migratory movements (Aebischer et al., 1996; Forstmeier, 2002). Individuals may adopt strategies whereby they return to occupy breeding sites earlier and more often than conspecifics to ensure they secure a higher quality breeding site (Morrison et al., 2019). As a consequence these individuals may then breed more successfully (Bêty et al., 2004). Indeed, to obtain these benefits occupancy behaviour may commence well in advance of the breeding season (MacDonald,

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1980). Nonbreeding occupancy of breeding sites may then be undertaken sporadically from the point of first return (Wails et al., 2020). Despite the benefits of this behaviour, individuals may vary in both their timing and pattern of occupancy (Brambilla & Bionda, 2013; Wails et al., 2020). While investment in occupancy is likely to have consequences for individual fitness, understanding is limited regarding how and why individuals vary in their timing and pattern of nonbreeding site occupancy behaviour. Traits such as sex may explain some variation in occupancy behaviour, with males generally returning earlier to sites and defending them more regularly than females (Fraser et al., 2002; Huffeldt & Merkel, 2016), although this has not been tested comprehensively in the nonbreeding season.

The timing of an individual's return to breeding sites and their occupancy pattern thereafter may also be influenced by their distribution prior to and following their return. Individuals remaining nearer to breeding sites during migration may be able to return to sites earlier than conspecifics (Schwemmer et al., 2021), and may consequently experience the greatest benefits. However, where breeding sites are distinct from foraging areas, as in many colonially breeding species, individuals are unlikely to continuously occupy the site following their return from migration, because of the need to forage, akin to central place foraging (Olsson et al., 2008). Foraging nearer to breeding sites can result in shorter foraging trips (Boyd, 1999), and therefore more time available for occupancy of breeding sites, with potential fitness benefits (Bennett et al., 2022). Nevertheless, there may only be limited food near breeding sites, meaning those individuals that are more able to outcompete others for finite food resources nearer breeding sites may then be able to occupy sites more often, have shorter bouts of absence and so benefit more greatly from occupancy (Margalida & Bertran, 2005). However, currently we have limited empirical information on how occupancy behaviour relates to nonbreeding distribution both before and after the first return to breeding sites. Additionally, we do not yet understand how an individual's ability to benefit from occupancy may be further influenced by their capacity to absorb costs associated with this behaviour in the form of lost foraging time.

Finally, undertaking occupancy may affect how individuals allocate their energy and time to other behaviours on a daily scale. Where individuals must move between breeding sites and foraging grounds, greater time and energy may be allocated to commuting behaviours such as flight (Dunn et al., 2020; Hull et al., 2001). To compensate, less time and energy may be allocated to other behaviours such as time spent resting on that day. Where occupancy-associated behaviours, such as commuting, have a higher energetic cost than other behaviours, we would then expect energetic expenditure to increase on days with occupancy, even if occupancy itself may have a low energetic cost (Viera et al., 2011). Individuals may then have to compromise in the extent to which they carry out this behaviour and subsequently face a trade-off between the 'pull' of occupancy and the 'push' of needing to forage. More efficient foragers that are able to obtain the energy that they require to sustain occupancy in a shorter period of time may then be able to spend longer occupying sites than poorer quality individuals (Viera et al., 2008). Yet, the energetic costs of nonbreeding site occupancy and how occupancy may influence the time available for other behaviours are also currently unknown.

Common guillemots, *Uria aalge* (hereafter 'guillemots'), are a colonially breeding seabird that, in at least part of their range, undertake a migration followed by nonbreeding season site occupancy. Guillemots nest at one of the highest densities of any bird species (Birkhead, 1978), show high levels of site fidelity and will actively defend sites both during and immediately after the breeding season (Harris & Wanless, 2003). All guillemots undertake a migration during which they remain at-sea for several weeks to moult their flight feathers (Harris & Wanless, 1990), and during which males provision their chicks at-sea (Dunn et al., 2019; Gaston & Jones, 1998). In colonies towards the southern extent of their range, they may then undertake a subsequent period of nonbreeding occupancy of breeding sites that may span up to 6 months (Ainley & Boekelheide, 1990; Harris, 1984; Sinclair, 2018). In colonies where nonbreeding occupancy is known to occur birds generally return to breeding sites to begin nonbreeding occupancy in mid-autumn and attend sporadically thereafter (Bennett et al., 2022; Dunn et al., 2020). However, the relative drivers and costs of nonbreeding occupancy behaviour in guillemots remain understudied.

Individual guillemots vary in the frequency and timing of nonbreeding season occupancy behaviour, suggesting a trade-off between costs and benefits. Guillemots breeding at sites that are occupied earlier and more often in the nonbreeding season benefit from earlier and more successful breeding (Bennett et al., 2022). Guillemots may vary greatly in how far away from breeding colonies they migrate during the nonbreeding season, in some instances migrating as far as 2500 km (Buckingham et al., 2022; Harris et al., 2015). How the timing of return to the colony relates to nonbreeding at-sea distribution in guillemots prior to their first return and their subsequent occupancy pattern is also not understood. Neither is it known whether guillemots incur a net cost of occupancy through increased energetic expenditure, for example due to commuting between the foraging and breeding sites. Such flight costs are likely to be particularly high in guillemots due to their high wing loading (Thaxter et al., 2010). Therefore, any increase in the time spent in flight through undertaking regular commuting flights between the colony and foraging grounds can significantly increase daily energy expenditure (Dunn et al., 2020). This commuting time may also have further consequences for the time and energy available for other behaviours, presenting individuals with a potential trade-off between occupying sites and having sufficient time to forage (Hatchwell, 1988a). Individuals that are able to remain nearer to the colony between periods of occupancy and forage more efficiently may be able to undertake occupancy more often and so be more likely to experience fitness benefits. Guillemots that demonstrate occupancy behaviour therefore present an ideal study system in which to investigate the variation in occupancy and how this may relate to nonbreeding distribution, energetics and the time available for other behaviours.

Here, we quantified individual variation in the occupancy of breeding sites in the nonbreeding season using data from a population of common guillemots breeding on the Isle of May, east Scotland, U.K. Guillemots at this colony start occupying breeding sites in the nonbreeding season from mid-October onwards with some sites occupied almost every day thereafter (Bennett et al., 2022). The high level of investment in occupancy observed at this colony enables an evaluation of the potential trade-offs that occupancy may present for individuals with respect to distribution and energetics. We investigated how variation in occupancy is related to distribution both during and after the moult migration and to individual energetics and behaviour allocation. We tested the following hypotheses and predictions.

We first hypothesized that individual site occupancy will vary with at-sea distribution (H1). From H1 we predicted that (1) individuals that moult closer to the colony will return earlier than those moulting further away (H1a) and (2) after birds have returned to the colony, termed the occupancy period, individuals remaining closer to the colony will have shorter bouts of absence (H1b). Second, we hypothesized that individuals will experience a cost of occupancy and vary in their ability to mitigate these costs (H2). From H2 we predicted that (1) daily energy expenditure of

individuals will be higher on days when they occupy their site (H2a), (2) the increase in energetic expenditure will result from increased time spent in costly flight behaviour to commute to the colony and less time in active and inactive behaviours at-sea (H2b) and (3) individuals that spend more time occupying their site on a given day will spend less time foraging (H2c).

METHODS

The data in this study were collected in 2018–2021 from a group of common guillemots breeding on a single cliff ledge on the Isle of May National Nature Reserve in the Firth of Forth, U.K. (56° 11′N, 02°33′W). We defined the nonbreeding season as beginning when birds first departed the colony after breeding and ending on 31 March, about a month before the first eggs are laid, that is, when breeding behaviour commences (Birkhead & Nevo, 1987).

Biologger Set-up

Guillemots were fitted with an archival geolocator immersion logger (MK3006 Migrate Technology Ltd, https://www.migratetech.co.uk/, hereafter 'GLS'), mounted on a plastic ring attached to the bird's leg. Loggers were deployed on 28 and retrieved from 19 individuals yielding data for three nonbreeding seasons. For a subset of individuals, we retrieved data from multiple years ($N = 17$ individuals in 2018–2019, $N = 14$ in 2019–2020 and $N = 6$ in 2020–2021; see Table A1 for details). GLSs were programmed to log light levels every minute with the maximum light level in every 10 min period being recorded (an arbitrary value of 0, 'dark', to 64, 'light'). Immersion in salt water was detected every 3 s with the frequency of 'wet' (immersed in salt water) logged for every 10 min period recorded (a value of 0, 'dry', to 200, 'wet'). Temperature (°C) was recorded as the sampled temperature at the end of 20 min periods when the tag had been continuously 'wet'. We did not undertake calibration of the GLSs as calibration is no longer recommended (Bråthen et al., 2021).

A subset of individuals were fitted with a time–depth recorder (TDR, model G5, Cefas, TDR, https://www.cefas.co.uk/) in addition to a GLS ($N = 8$ tags retrieved/9 deployed) for the 2019–2020 nonbreeding season (July 2019 to March 2020). TDRs were similarly attached via cable ties to a plastic attachment ring on the opposite leg to the GLS. TDRs sampled temperature and depth every 12 s, on every fifth day, with depths >1 m considered to indicate diving/foraging behaviour. In one individual the GLS wet/dry function malfunctioned prematurely resulting in recovery only of spatial data resulting in a final sample size of seven individuals with both GLS and TDR data.

Ethical Note

Feather samples, for sexing, and biologger data were collected under permits from the Home Office (Project licence number: PEAE7342F) and the British Trust for Ornithology (Special Methods licence number: 4671) respectively. All data were collected under an annual site-specific licence from NatureScot (Licence: MON/RP/181) and its predecessors. All biologgers were archival, meaning that tagged birds had to be caught on a second occasion to obtain behavioural and locational data for the interval between captures. To fit individuals with biologgers, and for biologger retrieval, birds were caught using a noose pole during chick rearing, or with a mist net in the prebreeding period. Time between capture and release of an individual was always <10 min. The biologgers used in this study weighed 0.48% (GLS, 3.7 g) and 0.56% (TDR, 4.5 g) of the minimum recorded body mass in a breeding adult guillemot recorded at the study site (765 g; Harris et al., 2000), so complying with

recommendations to minimize the relative weights of biologgers (Casper, 2009).

We are unable to make any comprehensive assessment of effects of logger deployments on survival rates in any year due to an insufficient sample size. However, all individuals tagged in 2018 were observed breeding at the colony in 2019 ($N = 17/17$). We were unable to assess return rates in 2019–2020 and 2020–2021 or breeding success for the 2020 breeding season, as we collected insufficient breeding data for tagged birds due to Covid-19 pandemic-related restrictions to the field site early in the 2020 season. However, we were able to compare breeding success during the 2019 breeding season, when birds were carrying only GLS loggers during the preceding nonbreeding season (2018–2019). Breeding success was marginally, but not significantly, lower for tagged individuals in 2019 (70.6%, $N = 12/17$ individuals) compared to untagged individuals on the same ledge (85.7%, $N = 30/35$ individuals; Z test: $\chi^2 = 0.85$, $P = 0.36$). On recapture, no individuals showed any damage to their legs because of device attachment.

Quantifying Occupancy Using GLS Data

We determined a bird was present at the colony on a given day if the GLS recorded two consecutive 10 min periods of being 'dry' ($\leq 4/200$; Fayet et al., 2017) and completely 'light' (64/64). We assume that these thresholds excluded flight behaviours as guillemots in the study region are known to not regularly undertake flights longer than 20 min during the nonbreeding season (Dunn et al., 2020). To verify this method we also identified days when individuals were present on their sites using concurrent time-lapse photography images of the same study individuals every 15 min in the 2018–2019 nonbreeding season ($N = 9$, Bennett et al., 2022). We found that the GLS-derived occupancy was in agreement with the camera-derived occupancy on $92 \pm 4\%$ of days across individuals ($N = 788/861$ days). When comparing the first return date there was a slightly larger discrepancy with GLS-derived return dates typically being later (mean difference between GLS and camera-derived return date = 8.87 days; minimum disagreement for an individual: 1; maximum: 28). To account for this larger discrepancy, we specifically incorporated the uncertainty around the GLS-derived return date into all relevant models (below). Hence, we are confident that GLS-derived occupancy is a reasonable measure for identifying days with occupancy across the nonbreeding season. We used these same criteria to determine when an individual departed the colony at the end of the breeding season, such that departure date was the first day without two consecutive records of 'dry' and 'light'. Consequently, we used the GLS-derived occupancy in all analyses. We tested whether varying the number of consecutive 10 min periods of 'light' and 'dry' could reduce any discrepancy with the camera-derived occupancy. Using two consecutive periods provided the smallest discrepancy with the camera-derived data. For full details of this method and comparison to camera-derived occupancy, see Appendix 1, Tables A2 and A3 and Fig. A1.

We divided the nonbreeding season into two periods. The moult period started on the date that individuals departed the colony after breeding and ended on the day before they first returned to the colony during which time birds will have undertaken their main moult of flight feathers (Glew et al., 2018). The occupancy period then started on the date that individuals first returned to the colony, by which time all birds would also be in their 'winter plumage', that is, with a largely white face and black auricular stripe, and ended on the last day of the nonbreeding season (31 March). We refer to whether an individual was absent from or present at the colony on a given day of the occupancy period as their 'occupancy status'.

Deriving Locations Using GLS Data

To investigate the nonbreeding distribution of individuals we estimated coordinate locations using the 'GeoLight' package in R resulting in two locations a day (Lisovski & Hahn, 2012). Although GLSs also recorded at-sea temperature data, which can be used to help refine location estimates, location estimates derived using the R package 'probGLS' (Merkel et al., 2016) were less accurate in our specific case than Geolight when compared with known locations (i.e. camera-derived colony presence). GeoLight first estimates the associated twilights for each day using the threshold method (Lisovski et al., 2020). We then applied a distance filter of the maximum distance that an individual could move at 69 km/h (Thaxter et al., 2010) using the 'distanceFilter' argument. We then also removed any locations 10 days either side of both the autumn and spring equinoxes due to unreliable latitude estimates during this period. Lastly, we obtained two coordinate positions per day, for 'dawn' and 'dusk', using the 'coord' argument and applying sun elevations derived from the 'getElevation' argument.

Processing GLS Locations

Individual estimates of daily position made from GLS are subject to the inherent error of locations derived from GLS using light data only (mean error 186 ± 114 km; Phillips et al., 2004). To counter this we used several commonly used approaches to process our GLS location data and increase the accuracy of location estimates that are suitable for the research questions we posed (e.g. the inclusion of 15 individual location estimates in a centroid decreases error from 193.5 ± 12.9 km to 94.5 ± 3.7 km; Bennett et al., 2024). To describe the spatial distributions of birds in relation to nonbreeding period and occupancy status we used GLS-derived coordinate locations to obtain 50% kernel utilization distributions using the 'adehabitatHR' package in R (Calenge, 2006). We estimated kernels for each study year, for the moult period and for when birds were present and absent during the occupancy period. We quantified the distance from the colony when birds were present at the colony in the occupancy period for completeness and context only. To summarize these distributions, we calculated the centroid of the 50% kernels for each year for each occupancy period. We also established whether we had a sufficiently large sample size of individuals to estimate robust kernels by quantifying sensitivity of the kernels estimated in each nonbreeding season to changes in sample size. In all cases we had a sufficiently large sample size to obtain a robust kernel (see Appendix 2 for further methodological details).

To investigate individual movement strategies (H1) we calculated the distance between the mean centroid locations estimated from the location data for each individual and season and the breeding colony for the moult period (H1a) and for occupancy status in the occupancy period (H1b). To account for the curvature of the earth we used the haversine great circle distance.

Calculation of Daily Energy Expenditure (DEE)

To investigate whether occupancy status affected the time and energy individuals allocated to behaviours (H2), we used the data from individuals that were fitted with both a GLS and a TDR. Individuals differed in the number of days with TDR data (see Table A4). We used the light, immersion in salt water and temperature data from the GLSs, and the depth (m) (converted from bars of pressure) and temperature data recorded by the TDRs. Using these measures in a decision tree process and following methods developed in similar studies (Buckingham et al., 2023; Elliott & Gaston, 2014; Linnebjerg et al., 2014), we determined the time

(min) spent in each of the following five behaviours on each day: flight, colony occupancy, diving (the time spent underwater), active on water (e.g. swimming) and inactive on water (i.e. resting). See Appendix 3, Table A4 and Fig. A2 for full details on this procedure.

We then calculated the daily energy expenditure (DEE) of individuals on every fifth day of the nonbreeding season using the following equation which assigns an energy cost in kJ for the time spent in each behaviour, as per Elliott and Gaston (2014) and Patterson et al. (2022):

$$DEE = 508\, T_f + 33\, T_o + 3.64 \sum \left[1 - e^{\frac{-T_d}{1.23}} \right] \\ + (113 - 2.75 \times SST)T_a + (72.2 - 2.75 \times SST)T_i$$

where T_* represents the minutes spent in each behaviour ('f' = flight, 'o' = site occupancy, 'd' = diving, 'a' = active on water and 'i' = inactive on water). 'SST' represents the mean sea surface temperature during each behaviour bout.

SST is included in the above equation to account for the greater thermal conductivity of water compared to air, which means that the lower critical temperature (LCT) is higher in water than in air. In the equation, we consider guillemots that exceed their LCT in the water (15°C; Croll & McLaren, 1993) to be thermoneutral. Hence, when SST exceeded 15 °C we considered inactive behaviour on water, T_i, to have the same energetic cost of inactive behaviour on land, T_o ($N = 10/167$ or 5.99% of bird-days).

Molecular Sexing of Individuals

Three breast feathers were sampled from all individuals fitted with biologgers for molecular sexing. Molecular sexing was undertaken by personnel at the NEOF Visitor Facility at Sheffield using an ABI sequencer (Griffiths et al., 1998). Across the three study nonbreeding seasons, seven females (F) and 12 males (M) were tagged (2018–2019: 7F, 9M; 2019–2020: 5F, 8M; 2020–2021: 2F, 4M); we were unable to identify the sex of one individual in 2018–2019 and a second individual in 2019–2020.

Statistical Analysis

All analyses were carried out using the statistical software R Version 4.1.1 (R Core Team, 2023) and are outlined in Table 1. For the majority of tests, we used a frequentist approach; however, for H1a we used Bayesian methods to incorporate known uncertainty in GLS-derived return dates within the analysis.

Initial summary: individual variation in the timing and pattern of occupancy

Prior to the main analysis, we first summarized individual occupancy timing and patterns.

To summarize individual nonbreeding occupancy patterns we created three measures of occupancy timing and four measures of occupancy status pattern for each individual in each nonbreeding season (Table 2). Occupancy timing measures were departure date and return date, and the difference (the number of days) between these two dates was termed the 'moult period duration'. For measures of occupancy status pattern, we first identified days in the occupancy period when an individual had occupied a site ('present') and days without occupancy for each individual ('absent'). We then classified these series of individual occupancy status into 'bouts' of consecutive days of absence or presence. From these bouts for each bird for each year we classified the first and second measures of occupancy patterns as the total frequency of bouts of absence/presence, and the third and fourth measures as the mean duration of bouts of absence and presence.

Table 1
Statistical specifications for the main analyses

Section	Test	Variable structure	Random effects	Error distribution	R package	Parameters
Initial summary	LMM	Occupancy pattern/timing measures ~ Sex		Gaussian (SW range: $W = 0.13$-0.56, $P = 0.12$-0.76)	lme4 (Bates et al., 2001)	
Hypothesis 1	Tukey test	Centroid distance from the colony ~ period (moult, occupancy: absent, occupancy: present)	Individual ID (I), Season (I)	Gaussian (SW: $W = 0.65$, $P = 0.21$)	lme4	
	LMM	Log (Moult period duration) ~ centroid distance from the colony	Season (I)	Gaussian + known error term for response (SW: $W = 0.87$, $P = 0.08$)	jagsUI (Kellner, 2021)	900 000 iterations 1 thinning interval 3 chains 200 000 burn-in
	GLMM	Log (Duration of absence bout) ~ centroid distance from the colony	Individual ID (IS), Season (I)	Gamma (log link)	lme4	
Hypothesis 2	LMM	DEE ~ occupancy status	Individual ID (I)	Gaussian (SW: $W = 0.99$, $P = 0.69$)	lme4	
	GLMM	Proportion of time in behaviour ~ occupancy status	Individual ID (I)	Beta (logit link)	glmmTMB (Brooks et al., 2017)	
		Proportion of DEE in behaviour ~ occupancy status	Individual ID (I)	Beta (logit link)	glmmTMB	
		Log (Time in flight) ~ Time in occupancy* Day length	Individual ID (I)	Beta (logit link)	glmmTMB	
		Time foraging ~ Time in occupancy* Day length	Individual ID (I)	Beta (logit link)	glmmTMB	

Letters in parentheses following random terms denote the best supported random effect structure, either an intercept, 'I', or a combined intercept and slope, 'IS'. LMM = linear mixed effects model. GLMM = generalized linear mixed effects model. 'SW' indicates a Shapiro-Wilks test for normality.

Lastly, we tested whether males and females differed in their occupancy pattern and timing (Table 1).

Hypothesis 1: individual site occupancy will vary with at-sea distribution

We initially investigated differences in distance from the colony between the moult period and the different occupancy statuses (present, absent) during the occupancy period (Table 1). For our first prediction, H1a, we tested whether individuals that remained closer to the colony during the moult period had a shorter moult period duration. We used the moult period duration as the response variable as opposed to the raw return date of individuals to account for individual differences in departure date from the colony which may influence how long individuals took to return, and therefore how far they travelled. Prior to modelling, to confirm that moult period duration remained reflective of an individual's return date to the colony (the measure known to have key life history benefits for individuals, Bennett et al., 2022), we tested the correlation between these two variables and demonstrated that they are closely related (Pearson $r = 0.89$, $N = 30$, $P < 0.01$). Consequently, we are confident that moult period

duration is reflective of the life history benefits associated with occupancy while accounting for individual differences in departure date. Since we had estimates for the error associated with estimating first return data, we used a Bayesian framework to account for this known error in our response variable. We assumed the derived estimates for 'moult period duration' had a Gaussian probability distribution, with known error (standard deviation of observed error in GLS estimated return date, Appendix 1).

We modelled observations for moult period duration for each centroid for each group, Y_i, derived from GLS data with known error, τ, where τ was derived from the standard error of the residuals for the calculated moult period duration, assuming a Gaussian distribution:

$$Y_i \sim \text{Normal}(\mu_i, \tau)$$

Estimates for moult period duration, μ_i, were modelled with a linear regression including a fixed effect for distance from the colony (km) for each individual in the moult period, X_i, and a categorical random effect for nonbreeding 'season' year, Season$_j$, where $j = 2018$−2019, 2019−2020 and 2020−2021 to account for interannual variation in all measures.

$$\mu_i = \alpha + \beta_i X_i + \text{Season}_j + \varepsilon$$

Parameter 'α' is a global intercept term, 'β_i' is the coefficient for the mean 'distance from the colony', X, during the moult period for observation 'i', and 'ε' denotes a residual process error term. Parameters 'α', 'β_i' and 'Season$_j$' were assigned minimally informative priors with a normal distribution with a mean of 0 and a precision of 0.0001, and ε with a gamma distribution with a mean 0.001 and a precision of 0.001.

For all parameters in the final model, the Gelman−Rubin statistic was >1 and <1.1 (Brooks & Gelman, 1998), and effective sample sizes were >400 indicating that models had converged with

Table 2
Summary statistics for occupancy measures averaged across all 3 study years

Measure	Mean	Minimum	Maximum
Timing			
Departure date	189±15 (3 July)	152 (1 June)	223 (10 Aug)
Moult period duration	111±30 days	72 days	228 days
Return date	299±26 (26 Oct)	274 (1 Oct)	53 (22 Feb)
Pattern			
Frequency of absences	14±7	1	31
Duration of absences (days)	5±8 days	1	97
Frequency of presences	15±7	1	31
Duration of presences (days)	3±3 days	1	28

Ordinal dates are provided with calendar dates in parentheses. $N = 35$ bird-years for all measures.

trace plots confirming good mixing of chains. The Gelman−Rubin statistic and effective sample sizes were calculated using the R package 'coda' (Plummer et al., 2006). We also visually inspected density and residual plots to confirm that model chains had converged and that residuals appeared randomly distributed.

We then tested H1b, that individuals that remain nearer to the colony during bouts of absence in the occupancy period will have shorter durations of absence (Table 1). We calculated distance as the mean centroid distance travelled from the colony in each bout of absence.

Hypothesis 2: individuals' ability to mitigate occupancy costs will vary

We tested H2a that DEE was higher on days with occupancy compared to days without occupancy in the occupancy period (Table 1). Occupancy status was again defined as whether individuals were absent from or present at the colony on that day. One individual was present at the colony every sampled day in the occupancy period and so no comparison could be made between DEE on days with and without occupancy for that individual. Time was a potentially confounding variable in this analysis since the calculation of DEE depends on SST, which will tend to increase as winter gives way to spring while the frequency of occupancy may increase (Bennett et al., 2022; Dunn et al., 2020). Thus, to test whether seasonal changes in SST influenced our result we repeated this model using DEEs recalculated using an SST value of 11.36 °C, the mean experienced across individuals throughout the nonbreeding season. These tests revealed the same direction and significance of relationships with a similar estimate as when using DEE calculated using the real-time SST data collected by the loggers (Δ estimate = 13.8 kJ, Appendix 4; Table A5; Fig. A3). Consequently, we are confident that there is no influence of time in this analysis.

We tested H2b that any increase in DEE on days with occupancy resulted from an increase in time apportioned to more energetically costly flight behaviour to commute to the colony and less time in inactive behaviour at-sea (Table 1). We considered the proportion of time and DEE allocated to diving behaviour to be synonymous with that allocated to foraging behaviour, as dives deeper than 1 m, our criterion for diving behaviour, are indicative of foraging attempts (Chimienti et al., 2017). We investigated how occupancy status affected how an individual allocated time and DEE between the behaviours flight, foraging, active and inactive on the water. We modelled both time and DEE in behaviours as proportions to account for the seasonal and individual variation in total DEE, and to make these results comparable.

To further investigate mechanisms underpinning this process, we then explored behaviours where allocation of time and/or DEE varied dependent on occupancy. We tested H2b, whether the time in flight varied with the time spent in occupancy, and H2c, whether the time in foraging decreased as time in occupancy increased. We included an effect of daylength to account for the temporal variation in the time available for these behaviours in daylight (Table 1).

Model validation

In all frequentist models that contained noncategorical explanatory variables we tested whether the inclusion of random intercepts, random slopes, or both random intercepts and random slopes for each random effect was most supported in the data by comparing Akaike's information criterion (AIC) scores. Frequentist models were fitted with restricted maximum likelihood (REML). We ranked models by their AIC score and then considered a model to have greater support in the data if it had an AIC score that was >2 smaller than the model with the next closest AIC (Appendix Appendix Table A6). We present the best supported model in all cases. In all models, we considered effects significant if their 95%

confidence intervals (95% CI) or credible intervals did not cross zero. We present the variance explained by fixed effects, marginal R^2, and by both fixed and random effects, conditional R^2, for all models obtained through the R package 'MuMIn' (Barton, 2020). We inspected residual plots for all models to ensure their distribution was random and checked all explanatory variables in final models for autocorrelation and disregarded any cases where this exceeded 0.7 (Dormann et al., 2013). We confirmed the normality of the residuals of models with an assumed Gaussian error distribution using Shapiro−Wilk tests and visual inspection of quantile−quantile plots. All means are presented ± SD unless indicated otherwise.

RESULTS

Initial Summary: Individual Variation in the Timing and Pattern of Occupancy

Individuals attended more frequently and for longer as the nonbreeding season progressed. Furthermore, individuals showed extensive variation in timing of their return to the colony, and in the duration and frequency of bouts of absence and presence after returning (Table 2, Fig. 1, Appendix Fig. A4).

Sex did not explain differences between individuals except that males left the colony earlier than females (estimate = −8.30, 95% CI = −15.0, −1.81; Appendix Table A7).

Hypothesis 1: Individual Site Occupancy Will Vary With At-Sea Distribution

Overall, individuals remained nearer to the colony in the moult period (166 ± 92 km), and during presence in the occupancy period (154 ± 131 km), than during absence in the occupancy period (268 ± 199 km; Tukey test: moult: estimate = −86.4, P = 0.02; occupancy: present: estimate = 35.9, P = 0.05; Appendix Table A8; Fig. A5). During absence, individuals moved towards the south and east of the colony in the western part of the North Sea (Fig. 2, Appendix Fig. A5). Locations were centred more clearly on the colony during presence in the occupancy period and during moult (Fig. 3); there was no clear difference in the distance from the colony between these two periods (Tukey test: estimate = −50.0, P = 0.1; Fig. 2, Appendix Table A8; Fig. A5).

Individuals returned to the colony earlier when they travelled a smaller distance from the colony in the moult period; for each ~7 km further away that an individual moved, their moult period duration was 1 day longer (Table 3, Fig. 3a), supporting H1a. This relationship held in the absence of those outlier values with a distance from the colony of >1000 km (estimate = 0.002, 95% CI = 0.001, 0.003).

There was a small effect of how far individuals travelled in bouts of absence in the occupancy period on the duration of absence bouts; individuals were absent for an additional day for each 330 km further they travelled from the colony, so showing some support for H1b (Table 3, Fig. 3b).

In both models both the marginal and conditional R^2 scores were relatively low (maximum R^2: 0.41 for conditional effects in Table 3).

Hypothesis 2: Individuals' Ability to Mitigate Occupancy Costs Will Vary

There was no significant difference between the DEE on days when individuals were absent from or present at breeding sites (estimate = 73, 95% CI = −175, 325), in contrast to our predictions in H2a. The inclusion of individual random slopes was not
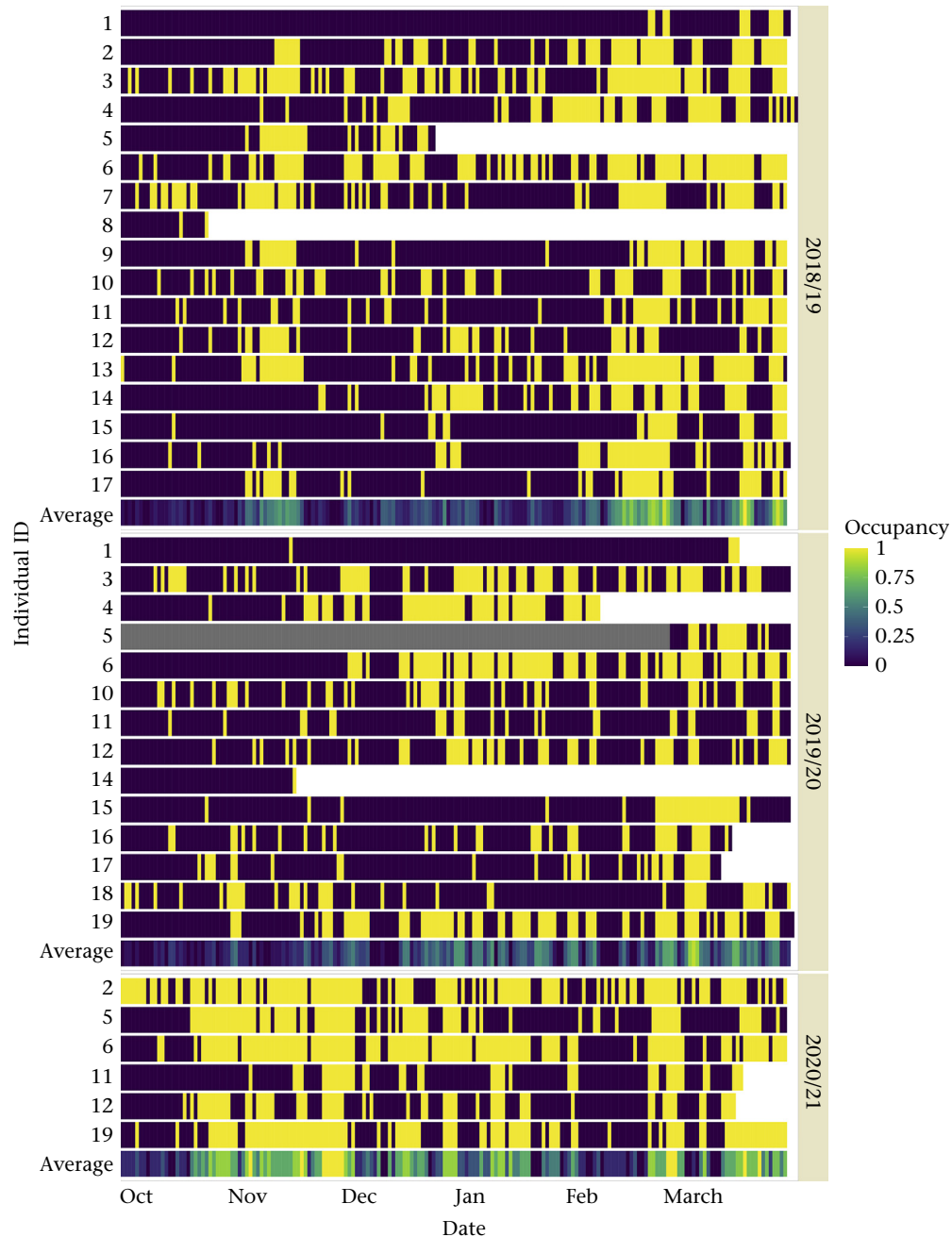
Figure 1. Individual daily occupancy patterns of presence, '1', and absence, '0', across three nonbreeding seasons from the earliest return date after moult of any bird (1 October). 'Average' is the mean occupancy pattern across individuals in each nonbreeding season. White spaces indicate days with no data due to logger malfunction. Grey spaces indicate periods prior to an individual being fitted with a geolocator within a season.

supported in the final model. Conditional effects alone accounted for only a minor component of model variance ($R^2 = 0.02$); however, the addition of individual random intercepts (Appendix Table A6) explained almost just over half of the model variance indicating considerable individual level variation in DEE ($R^2 = 0.51$).

In the occupancy period, individuals occupied sites for on average 9.3% of the time and occupancy accounted for 4.1% of DEE on days they were present. On these days they spent 2% less time foraging and 2% more time flying (foraging: standardized estimate $= -0.17$, 95% CI $= -0.32$, -0.02; flight: standardized estimate $= 2.16$, 95% CI $= 1.83$, 2.49; Fig. 4a). This is reflected in

allocation of energy to DEE: individuals allocated on average 2% less of their DEE to foraging (standardized estimate $= -0.23$, 95% CI $= -0.37$, -0.08) and 9% more of their DEE to flight (standardized estimate $= 2.18$, 95% CI $= 1.78$, 2.59; Fig. 4b). Consequently, we found some support for H2b that any increase in DEE will result from increased time spent in costly flight.

There was no significant difference in the proportion of DEE allocated to active (estimate $= -0.08$, 95% CI $= -0.53$, 0.36) and inactive (estimate $= -0.15$, 95% CI $= -0.57$, 0.26) behaviours on days with and without occupancy (Fig. 4b). This lack of difference in DEE reflects the lack of a difference in the proportion of daily time spent in these two behaviours (active: estimate $= -0.99$, 95%
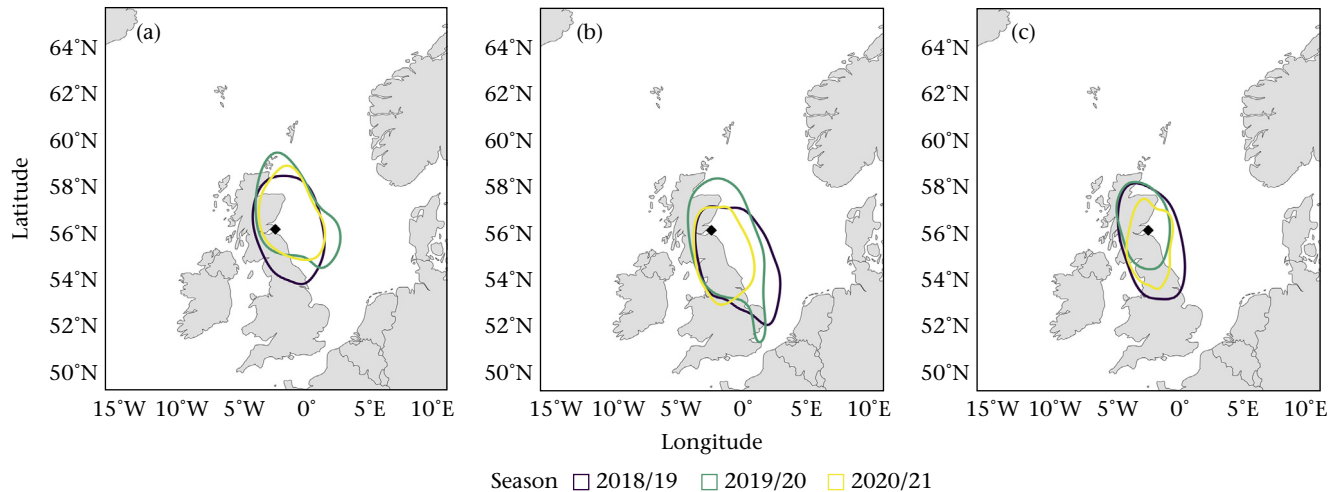
Figure 2. The 50% kernel distributions across individuals in (a) the moult period, the occupancy period when birds were (b) absent and (c) present in 3 study years. (a) 2018−2019, (b) 2019−2020 and (c) 2020−2021 for the three periods (moult, the occupancy period when birds were present and the occupancy period when birds were absent). A black diamond indicates the location of the study colony. $N = 17$, 14 and 6 individuals in each season, respectively.
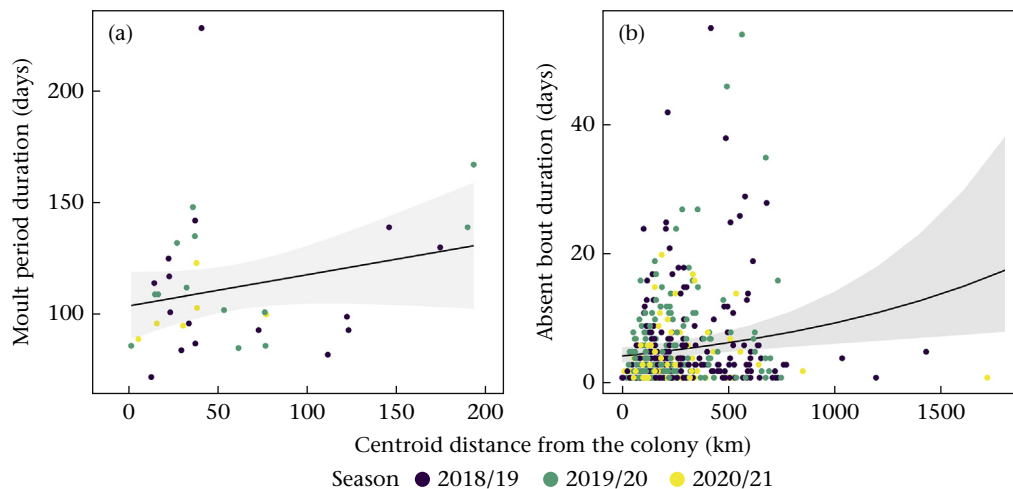

Figure 3. The relationship between the distance travelled from the colony and (a) moult period duration and (b) the duration of bouts of absence from the colony in the occupancy period in three nonbreeding seasons. Data are indicated by points and (a) LMM and (b) GLMM predictions ± 95% (a) credible and (b) confidence intervals by a fitted line and shaded area, respectively. $N = 31$ and 448 observations, respectively, and 18 individuals.

CI $= -2.84$, 0.54; inactive: estimate $= -0.29$, 95% CI $= -0.70$, 0.12; Fig. 4a). The inclusion of individual random slopes was not supported in both models, indicating that individuals adjusted their DEE similarly in relation to occupancy status (Appendix Table A6). All individuals showed the same direction of changes in the proportion of DEE allocated to flight and foraging.

In all models, except those for flight, marginal effects accounted for only minor components of model variance. The time in flight therefore explained a greater proportion of model variation (range of marginal R^2 excluding flight: 0.003−0.07; including flight: 0.60−0.65; Appendix Table A9). In all models the addition of the individual random slope conditional effect explained almost all variance, highlighting the individual level variation in allocation of time and energy to different behaviours (range of conditional R^2: 0.89−0.98).

All individuals experienced a trade-off in the time available for foraging in response to occupancy; the more time that an individual spent in occupancy on a given day, the greater the reduction

in time spent foraging on that day such that for each hour in occupancy individuals spent ~24 min less in foraging, so supporting H2c (Table 4, Fig. 5). In contrast, the proportion of time spent in flight on days with occupancy was consistent irrespective of the time spent in occupancy (Table 4). In contrast to previous models, individual random slopes were not supported in either final model (Appendix Table A6). Therefore, individuals had similar relationships between time in occupancy and time in foraging and flight. Daylength and the interaction between daylength and time in flight/foraging had no effect in either model; consequently, the relationships we observed occur independent of temporal variation in daylength.

The time spent foraging explained a much greater proportion of model variance than time in flight, highlighting the strength of the relationship of the former with the time in occupancy (marginal R^2: time foraging $= 0.24$; in flight $= 0.01$; Table 4). In both models the conditional R^2 indicated that the inclusion of the random intercept of individual ID explained more than half of model variance

Table 3
Outputs from LMMs assessing the effect of the mean distance travelled from the colony on the duration of the moult period, in a Bayesian framework, and bouts of absence, in a frequentist framework

Fixed effects	Estimate	SD	95% CI
Distance from colony (moult)			
Intercept	103.18	8.32	86.84, 119.42
Distance travelled (km)	**0.15**	**0.10**	**0.03, 0.34**
Random effect variances			
Season (2018−2019)	0.01	0.43	
Season (2019−2020)	0.02	0.34	
Season (2020−2021)	−0.01	0.7	
Residual variance	28.21	3.91	
Marginal R^2=0.07, conditional R^2=0.41, N=35 observations, 18 groups			
Distance from colony (absence)			
Intercept	**5.01**	**1.12**	**2.91, 7.22**
Distance travelled (km)	**0.003**	**0.001**	**0.002, 0.004**
Random effect variances			
Individual ID	**0.001**	**0.001**	
Season	0.03	0.60	
Residual variance	0.76	0.87	
Marginal R^2=0.06, conditional R^2=0.32, N=511 observations, 18 groups			

Significant terms, i.e. those with 95% credible (distance from colony (moult)) or confidence intervals (distance from colony (absence)) not overlapping zero, are in bold.

(conditional R^2: model a = 0.56; model b = 0.67) indicating that the direction and strength of these relationships for individuals may vary.

DISCUSSION

Using a novel approach to identify occupancy of breeding sites in the nonbreeding season we made the first quantification of individual level patterns of occupancy throughout the nonbreeding season and related them to at-sea distribution and energetics. Individuals varied in their occupancy timing and patterns and individuals that remained nearer to the colony returned to occupy sites earlier and had shorter durations of absence thereafter (H1a, b). Consequently, remaining nearer to the colony was advantageous. Importantly, there was no overall energetic cost associated with occupancy (H2a). Rather, occupancy affected how individuals allocated their behaviour, such that on days with occupancy individuals spent less time foraging and more time flying indicative of commuting to and from the colony (H2b). Individuals may have differed in their capability to balance time spent in nonbreeding site occupancy with time spent in foraging as when investment in occupancy increased investment in foraging decreased (H2c).

Individuals varied in the distances that they travelled from the colony both prior to their first return after moulting and subsequently during the occupancy period. Individuals that remained nearer to the colony during their moult returned to sites sooner and were away for shorter durations thereafter. Both distance and time effects were consistent across individuals; however, the effect of distance on the time taken to initially return to the colony was much stronger. Both an earlier return to breeding sites and more days spent in occupancy are associated with earlier and more successful breeding. Our results support other studies that have demonstrated a link between timing of return and breeding success (Bennett et al., 2022; Norris et al., 2004; Velmala et al., 2015). As such, this behaviour may have a greater fitness consequence than the proportion of days spent in occupancy (Bennett et al., 2022). By extension, remaining nearer to the colony may then also be beneficial, as this can influence when individuals return to breeding sites (Smallegange et al., 2010). Individuals that can outcompete others for foraging areas nearer to the colony may then be better placed to undertake occupancy. Conversely, individuals may be limited in the distance they can travel from the colony, as in central-place foraging (Olsson et al., 2008), if they are to reap the benefits of occupancy. The suggestion that some individuals are able to remain within 200 km of the colony throughout the winter also shows that local foraging and environmental conditions are sufficiently favourable to support a proportion of the population (Dunn et al., 2022). There is evidence that resident individuals may gamble on enduring potentially lower quality local prey resources to benefit from remaining nearer breeding sites (Boyle, 2008), although how variation in local environmental conditions and prey availability affects occupancy is not well understood. Were local conditions to decline, occupancy may become viable for a smaller proportion of individuals, and potentially more costly for all. None the less, note that the distances travelled in the moult period and in bouts of absence after return to the colony explained comparatively little of the variation in the duration of the moult period and bout of absence. This lack of a strong effect may either have resulted from the imperfect precision in the GLS we used or be indicative of a true weak effect. Clearly, future work using biologgers with greater precision will be required to elucidate this further. Overall, it is clear that how behaviours such as occupancy relate to distribution needs to be investigated further. This area of research will be increasingly pertinent given the increase in the prevalence of occupancy of breeding sites in the nonbreeding season in this study population (Harris & Wanless, 2016).

Occupancy did not present an overall energetic cost for individuals, but it did affect how individuals allocated their time to behaviours. The absence of an increase in DEE on days with occupancy occurred despite an increase in the time spent in flight, associated with commuting to and from the colony, which increased on days with occupancy by 2%. The lack of an effect of occupancy on DEE likely resulted from the relatively low energetic cost associated with occupancy behaviour itself (Viera et al., 2011). The differing degrees to which individuals invested in occupancy further indicates that individuals may also vary in their ability to undertake occupancy. Longer durations of occupancy may also have a cumulative toll on individuals; male guillemots suffer from reduced body condition following intensive periods of occupancy just prior to breeding (Hatchwell, 1988b). However, more recent studies investigating the change in mass of guillemots throughout the winter do not show clear declines in mass concurrent with investment in occupancy in this population (Dunn et al., 2022; Harris et al., 2000). An individual's ability to undertake occupancy may then result not from their ability to absorb direct energetic costs of occupancy through changes in body mass alone, but rather from being better able to allocate time and energy to other key behaviours, such as foraging. Further, if we accept a simplifying assumption of a balanced DEE on each day for individuals, that is, energy expended is the same as energy gained, there is a positive relationship between the time allocated to occupancy and foraging efficiency (Fig. 6). Consequently, a foraging efficiency of 12 kJ/ min would allow birds to occupy sites for >300 min/ day compared with an efficiency of 7 kJ/ min facilitating <1 h of occupancy a day (i.e. a 71% increase in efficiency). The estimated difference in foraging efficiency required to spend longer periods occupying breeding sites, while relatively large, is well within the range estimated in other seabird species (Weimerskirch et al., 2003). However, it may well be the case that individuals undertaking occupancy for longer may both be more efficient foragers and be able to make short-term adjustments in body mass to compensate for losses in foraging time.

The ability of individuals to bear the immediate higher costs of occupancy, in terms of reduced foraging time, would then indicate that individuals undertaking frequent and lengthy durations of occupancy are of higher quality (Pinaud & Weimerskirch, 2005). We hypothesize that this might act via greater foraging capabilities
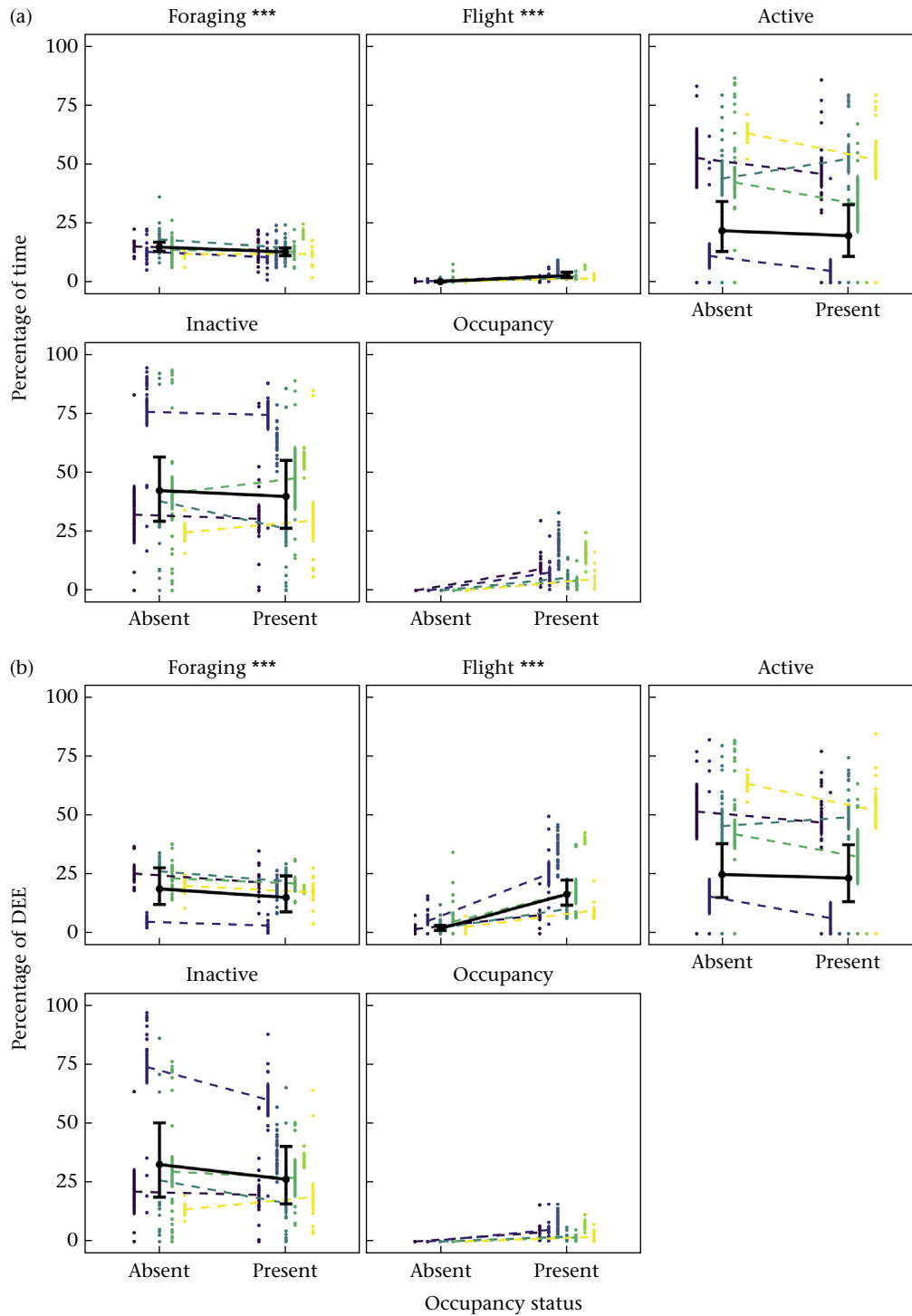
Figure 4. The percentage of (a) the time and (b) the daily energy expenditure (DEE), and associated SE (error bars) allocated to each behaviour type on days when individuals were absent or present at the colony during the occupancy period. Raw data for individuals are indicated by points. GLMM predictions are in black; other colours indicate individual ID. Group means are joined by dashed lines and are jittered to ease interpretation. ***$P < 0.001$. Observed percentages for 'Occupancy' behaviour are provided for context. $N = 167$ observations for each facet and 7 individuals.

of some individuals enabling them to occupy sites earlier and for longer (Grand, 1997). However, more frequent DEE estimates, and ideally measures or estimates of body mass, would be required to fully-separate the direct energetic costs that individuals may absorb through minor changes in body mass versus the foraging capabilities and therefore quality of individuals in relation to investment in occupancy.

Here we have demonstrated the relationship between nonbreeding site occupancy, distribution and energetics in a colonially breeding seabird. Our study may provide additional impetus to understand how occupancy of breeding sites in the nonbreeding season relates to other nonbreeding behaviours and the space use of individuals that may affect their exposure to threats at this time. Investigating these questions may be particularly important in

Table 4
GLMM outputs assessing the effect of the proportion of daily time spent in occupancy behaviour on foraging behaviour and the time spent in flight

Fixed effects	Estimate	SE	95% confidence interval
Proportion of time foraging			
Intercept	**−1.62**	**0.57**	**−2.74, −0.49**
Proportion of time in occupancy	**−11.14**	**4.37**	**−19.71, −2.58**
Daylength	0.01	0.05	−0.09, 0.09
Proportion of time in occupancy*daylength	0.62	0.35	−0.07, 1.32
Marginal R^2=0.24, conditional R^2=0.56, N=97 observations, 7 groups			
Proportion of time in flight			
Intercept	**−4.42**	**0.71**	**−5.80, −3.02**
Proportion of time in occupancy	−1.82	4.26	−10.16, 6.53
Daylength	0.08	0.05	−0.02, 0.20
Proportion of time in occupancy*daylength	−0.03	0.34	−0.70, 0.64
Marginal R^2=0.01, conditional R^2=0.67, N=96 observations, 7 groups			

Significant effects, i.e. those with 95% confidence intervals not overlapping zero, are in bold.
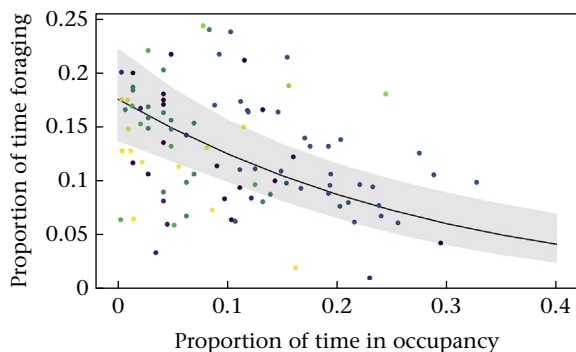
Figure 5. The proportion of daily time spent foraging in relation to the proportion of daily time spent occupying the colony. Colours indicate individual ID. GLMM predictions ± 95% confidence intervals are indicate by a fitted line and shaded area, respectively. $N = 97$ observations and 7 individuals.
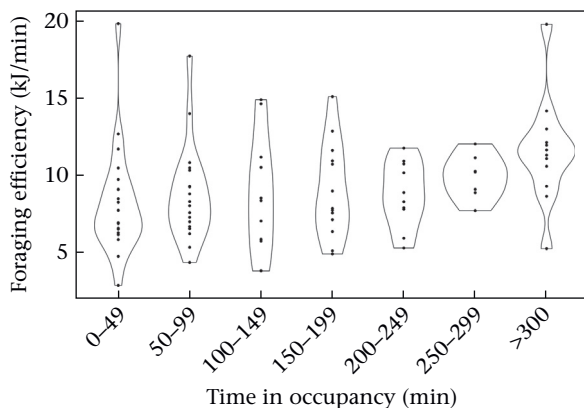
Figure 6. A violin plot of the hypothesized relationship between the daily time spent occupying breeding sites and the foraging efficiency of an individual on that day. $N = 96$ observations. Foraging efficiency was the total DEE per individual per day multiplied by an assimilation factor and divided by the time spent diving (i.e. foraging) on that day. The assimilation factor, the species-specific efficiency of energy intake to energy available to an organism to undertake behaviours and physiological processes, was 0.763, the mean of the two assimilation factors estimated for U.K. guillemots by Hilton et al. (2000).

guillemots given that while observations of this behaviour in this species are widespread (Harris & Wanless, 2016; Manuwal et al., 2001; Sinclair, 2018), colonies at which this behaviour has been quantified are few. To this end, we present evidence that individuals occupying sites earlier and more often and remaining

nearer to the colony may be of superior foraging and/or competitive abilities. Accordingly, the drive to obtain a higher quality breeding site can influence year-round behaviour and be indicative of individual quality. To understand the variation in, and the importance of, this behaviour future work should investigate the role of individual quality. Further, there are numerous examples of colonies where this behaviour is unlikely to occur to the extent observed in this study (Merkel et al., 2019), with some colonies hosting individuals that migrate much greater distances from the colony (upwards of 1200 km), both in guillemots and in the closely related thick-billed murre, *Uria lomvia*, (Patterson et al., 2021; Tranquilla et al., 2013). Future studies should investigate this and determine the causes of geographical variation in this behaviour.

Author Contributions

Data Availability

The data set used for this study is available in the Supplementary material.

Declaration of Interest

The authors declare no conflicts of interest.

Acknowledgments

Supplementary Material

Supplementary material associated with this article is available in the online version at https://doi.org/10.1016/j.anbehav.2024.07.023.

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Appendix 1. Comparison of GLS and Camera-derived Occupancy

As the time-lapse camera data contained data gaps and periods when a definite occupancy status could not be determined, we investigated whether the GLS tags alone could be used to determine daily occupancy (see Table A1 for numbers of tags deployed and retrieved).

To do this we compared the derived presences and absences from both the GLS and camera method with each other to determine whether the two produced comparable results for nine individual guillemots in 2018/2019 for which we had both data types available. Camera set-up was as described in Bennett et al. (2022).

We determined an individual to be 'present' using the geolocator data when the saltwater immersion logger was dry ('dry'; ≤4/200, Fayet et al., 2017), and the light sensor was completely light, ('light'; 64/64), for two consecutive 10 min bins to approximate the resolution of the camera data to which we were comparing. On days where these conditions were never met the individual was considered 'absent'.

We determined occupancy directly with the camera data as either 'present', 'absent' or with 'unknown' occupancy status. We considered an individual present if we could positively identify that individual at its breeding site by observing its colour ring combination ($N = 356/2848$ bird-days across nine individuals). We considered an individual to be absent if no birds were observed at the individual's breeding site ($N = 1421/2848$), or when a bird was present at the breeding site but it was always positively identified as the partner of the focal individual ($N = 78/2848$). Finally, we considered an individual to have unknown occupancy if one or more birds were present at the individual's breeding site, but it was

not possible to positively identify the bird(s) present as the focal individual or its partner as the colour ring combination of the bird(s) could not be seen ($N = 993/2848$). We then filtered the camera-derived occupancy data when we could confidently identify when birds were absent or present to just those days for which we also had GLS-derived occupancy data ($N = 861/2848$).

We found that the GLS-derived occupancy agreed with the camera-derived occupancy on an average of $91.88 \pm 4.12\%$ of days (range $85.71–97.91\%$, $N = 788/861$ bird-days across nine individuals). The agreement between the two methods was largely consistent between months demonstrating that there was limited variation in the reliability of the GLS-derived occupancy across the nonbreeding season (on average $91.89 \pm 3.61\%$ of records in each month, range $85.48–96.27\%$).

The majority of mismatches between the two methods were as a result of a 'false negative', for example the GLS method identifying the bird as absent when it was known to be present using the camera method or vice versa ($N = 39/73$ mismatched records). The higher prevalence of false negatives compared to false positives may result from the GLS method being less accurate at identifying occupancy when, for example, occupancy periods were shorter than the 20 min threshold that we used. However, the incidence of occupancy lasting less than 20 min, as recorded by the time-lapse data was low ($N = 11/1427$ bird-days when one or more individuals were present at a site in only one image on that day). The false positives that we identified in $N = 34/73$ of mismatches may arise from, for example, birds undertaking an infrequent flight with a duration of >20 min (Fig. A1).

From this and other studies, we know that guillemots only very rarely remain at the colony at night and first arrive at the colony on a given day soon after sunrise, departing later after a seasonally dependent duration of time of occupancy (Bennett et al., 2022; Harris & Wanless, 2016). Consequently, providing further support for the GLS method is that this method did not routinely identify occupancy at night ($N = 2/8577$ bird-days) or during a period beginning some while after sunrise ($N = 27/8577$ bird-days) or during multiple periods in a day ($N = 31/8577$ bird-days). As a result, we are confident that the GLS method is a suitable alternative method to determine the daily presence of individuals at the colony.

We then compared the first return dates to sites estimated by both methods. Here we were able to include a larger sample size of individuals as camera quality was sufficient in the early part of the season in all study years ($N = 13$ individuals). The GLS method estimated first return dates within an average of 8.87 ± 8.77 days of the true return date derived from the cameras (range $1–28$). Therefore, we are confident the first return date estimated by the GLS-derived method is also a reasonably accurate estimate given the wide range of camera-derived return dates (range 21 October–16 January). However, to account for this known discrepancy from the camera-derived occupancy, we account for this known error in all relevant models.

We also tested whether a higher or lower frequency of consecutive 'dry' and 'light' bins of the geolocator data showed greater agreement with the camera-derived occupancy data (Tables A2 and A3). Using the measure of 2 consecutive days, however, showed the greatest average agreement with the camera data for both the daily pattern of occupancy and the first return date estimated and so this is the measure we used in the analysis.

Appendix 2. Estimation of Required Sample Size for Geolocator-derived Distribution

We tested whether we had a sufficiently large sample size of individuals to robustly estimate the distribution of birds in each nonbreeding season. We constructed 50% kernel density distributions for the moult period and the occupancy period when birds were present, and absent, varying the sample size of individuals included from one through to the total number of individuals for which we had data in each category. The individuals included in each kernel were randomly selected with replacement. We then repeated this randomization procedure 1000 times. We then inspected plots of the sample size of individuals in relation to the median kernel contour area for each category. From this we determined the sample size at which the resulting curve reached an asymptote, i.e. an increase in the number of individuals included did not significantly increase the kernel contour area estimated, as per Buckingham et al. (2022) and Soanes et al. (2013). In all cases we had sufficient individuals required for the curves to reach an asymptote.

Appendix 3. Deriving Behaviour from GLS and TDR Loggers

We fitted eight individuals with both GLS (Biotrack, MK3006) and TDRs (CEFAS, G5) in the 2019–2020 nonbreeding season to determine the behaviours of individuals throughout this period (for date range of available data for individuals see Table A4).

First, we undertook a sense-check of the depths derived from the pressure sensor data from the TDRs. When at the surface the depth recorded should be 0 m, termed the 'baseline' in analyses of depth data. However, over time the baseline depth can drift (Elliott & Gaston, 2009). A drift in the baseline is important to detect, as this will affect the depth recorded for all future records leading to incorrect depth readings. As such we identified those time points when the baseline drifted and corrected those depths accordingly (Duckworth et al., 2020).

Owing to the sensitivity of the pressure sensor, spurious depth readings were occasionally recorded that indicated a dive speed that was beyond the maximum recorded for the guillemots (maximum potential distance covered in 12 s: 22.32 m (Thaxter et al., 2010), $N = 1675/2\,602\,201$ cases, 0.0006%). Where this occurred, we replaced these unreasonable depth readings with the mean of the dive depths of the previous and subsequent reasonable depth readings. Finally, we then categorized the depths into diving (a depth of >1 m) or at the surface (a depth of <1 m) as per Buckingham et al. (2023).

We then combined the GLS and TDR data into one data set. As the data from the loggers were recorded at differing temporal resolutions, we combined the data sets so that each GLS time point (every 10 min) was associated with the nearest subsequent TDR time point (every 12 s). We identified behaviours using a modified version of the approach taken in Buckingham et al. (2023).

Using these activity data from both the TDR and GLS devices we determined the time spent each day for each individual in the following five behaviours: T_d (diving), T_a (active on the water/swimming), T_i (inactive on the water/resting), T_f (in flight) or T_o (in colony occupancy). To assign behaviours we undertook an initial classification of the activity data followed by some further modifications resulting from the outcome of validation tests (see Fig. A2). We initially classified behaviours at a resolution of 12 s, before finally smoothing to the most common behaviour in each minute. For the purposes of classifying behaviours we determined the GLS tag to be 'wet' if the wet/dry reading was $\geq 4/200$ (Fayet et al., 2017).

First, we classified T_d as the time when the TDR depth was >1 m (Dunn et al., 2020). We then calculated the time that a bird spent in T_i as the time spent with one leg withdrawn into plumage, when resting on the sea (Linnebjerg et al., 2014). Because the birds had a TDR and a GLS on each leg, and we did not have the same activity data available from both tags, we had to determine the time spent

in T_i differently for either tag or leg. For the TDR we considered the time spent in T_i as when the temperature on the TDR tag was >18 °C ($T_{i\text{-TDR}}$), as when withdrawn into plumage the temperature of the tag increases (Robertson et al., 2012). We then estimated the time spent in $T_{i\text{-GLS}}$ during the night as the time when the GLS was 'dry'. This was likely to be an underestimate of the time spent in this behaviour as we were unable to tell whether this leg was 'wet' because the bird was active or because it was tucking in the other leg. We added a later modification step to address this. We also could not use the wet/dry data to estimate $T_{i\text{-GLS}}$ in the day time, as we could not distinguish between this and other 'dry' behaviours (T_f and T_o) which do not take place at night at our study colony (Bennett et al., 2022; Robertson et al., 2012). To estimate the time spent in $T_{i\text{-GLS}}$ in the day we investigated whether this behaviour had a unique signature. We found that the identified night $T_{i\text{-GLS}}$ behaviours showed a significantly lower variation in TDR temperature between successive readings than other behaviours (proportion of successive readings with a 0 °C change = 0.86 ± 0.03). Following this we also assigned readings where the proportion of 0 °C change was <0.83 to $T_{i\text{-GLS}}$.

After assigning time spent in $T_{i\text{-GLS}}$, we next considered the time spent in T_a to be the remaining occurrences when the GLS tag was 'wet'. Following this, we then undertook a modification step to reassign behaviours at night previously assigned as T_a to $T_{i\text{-GLS}}$. Here we ensured that the time spent in both $T_{i\text{-TDR}}$ and $T_{i\text{-GLS}}$ was equal, in the absence of knowing what degree of leggedness is present in guillemots (i.e. the favouring of tucking in one leg as opposed to the other, Fayet et al., 2017). First, we quantified the difference in the number of minutes that we had determined each individual spent in either $T_{i\text{-GLS}}$ or $T_{i\text{-TDR}}$ in each day. Next, we reassigned this difference in minutes from T_a to $T_{i\text{-GLS}}$. This correction resulted in the time spent in both $T_{i\text{-TDR}}$ and $T_{i\text{-GLS}}$ behaviours being equal. We then summed $T_{i\text{-TDR}}$ and $T_{i\text{-GLS}}$ to get our total time spent in T_i. If we found that prior to this correction the time spent in T_a was $<T_{i\text{-GLS}}$ we reassigned all T_a to $T_{i\text{-GLS}}$. Then we assigned T_0 as the time during

daylight that the GLS tag was 'dry' for ≥ 20 min as per our GLS-derived occupancy methodology. We considered all remaining time to be T_f, that is, when the GLS was 'dry' for a period of <20 min during daylight.

We then added an additional modification step to ensure that all bouts of T_c were preceded by a bout of T_f (as individuals must fly to access the colony). Where T_o was not preceded by T_f we reassigned the first 5 min of the T_o bout to T_f as this is the likely minimum flying time for individuals to commute to the colony based on our seasonal observations of their distribution within the Firth of Forth. We did not force behaviour order to also include a bout of T_f after T_o as individuals predominantly land immediately on the sea after leaving the colony (in <1 min of departing; Linnebjerg et al., 2014).

After assigning all behaviours, we undertook an additional validation to confirm our classifications. We examined whether our classifications resulted in any flight or occupancy behaviours during the core moult period for guillemots in this population (~mid-August–~mid-September) when the birds would have been expected to have been flightless (Harris & Wanless, 1990). We found that flight took place in 0.008% and 0.005% of samples during this period for flight and occupancy, respectively (N flight = 514/67 680 samples; N occupancy = 359/67 680 samples). Consequently, we are confident that the method has a low incidence of false positives for detecting flight or occupancy.

Appendix 4. DEE Estimates Using a Constant SST

To distinguish the increase in DEE from any seasonal effect of SST we repeated the DEE calculation presented in the Methods but holding SST as a constant. Here, we used the mean SST across the entire nonbreeding season and found that the result was qualitatively similar to that when using the raw SST values, such that there was a lack of evidence for a significant relationship between DEE and occupancy and a similarly sized estimate (Δ estimate = 8.15 kJ; Table A5; Fig. A3).

Table A1
Sample sizes of geolocator (GLS) deployment and retrievals

Year	Number deployed	Number retrieved
2018	21	NA
2019	19	12
2020	16	13 (4)
2021	0	9 (1)

Numbers in parentheses indicate the recapture of birds that were fitted with a logger >1 year previously that contained data for all preceding study years. Three of the birds recaught in 2021 did not yield data: two had lost their GLS and one GLS malfunctioned. NA: no tags were retrieved in 2018 as they were only deployed in that year.

Table A2
A comparison of camera and GLS-derived occupancy measures for estimating the daily pattern of occupancy where GLS-derived occupancy measures vary in the required frequency of consecutive 'dry' and 'light' records

No. of consecutive 'dry' and 'light' records	Mean±SD % agreement	Minimum % agreement	Maximum % agreement
1	85.23±7.36	73.27	95.83
2	**91.18±3.94**	**85.71**	**98.96**
3	90.48±3.87	86.17	98.96
4	89.31±5.97	77.94	98.96
5	72.77±17.08	32.35	89.58

The optimum method is shown in bold.

Table A3
A comparison of camera and GLS-derived occupancy measures for estimating the first return date where GLS-derived occupancy measures vary in the required frequency of consecutive 'dry' and 'light' records

No. of consecutive 'dry' and 'light' records	Mean±SD difference (days)	Minimum difference (days)	Maximum difference (days)
1	16.26±12.12	1	37
2	**8.87±8.77**	**1**	**28**
3	14.25±22.17	1	80
4	19.48±31.19	1	101
5	19.79±33.40	1	110

The optimum method is shown in bold.

Table A4
The range of dates for which there are combined TDR-GLS data available for individuals in the 2019–2020 nonbreeding season

Individual	First date	Last date
1	11 July	22 March
2	11 July	11 November
3	11 July	17 March
4	11 July	7 March
5	26 July	22 March
6	26 July	22 March
7	11 July	7 March
8	11 July	6 February

Table A5
Outputs from an LMM assessing the effect of occupancy on individual daily energy expenditure derived using a constant SST.

i	Estimate	SE	95% confidence interval
Intercept	**2645.90**	**262.70**	**2106.18, 3189.37**
Absent	64.60	116.20	−162.00, 295.11
	Marginal R^2=0.03, conditional R^2=0.51, N=167 observations, 7 groups		

Significant terms i.e. those with 95% confidence intervals not overlapping zero, are in bold. 'Present' was used as a reference level.

Table A6
Akaike information criterion (AIC) table of LMMs and GLMMs with different random effect term structures

Fixed effect structure	Random effect structure			AIC	ΔAIC
	Intercept	Slope	Combined intercept+slope		
Distance from the colony~Period	X			**149 078.5**	**0**
(moult, occupancy: absent, occupancy: present)		X		NA	NA
			X	NA	NA
	X	X		NA	NA
Duration of moult period~distance travelled	X			**339.57**[1]	**0**
		X		NA	NA
			X	NA	NA
	X	X		NA	NA
Duration of absent bout~distance travelled	X			**428.13**	0
	X	X		458.43	NA
			X	498.85[2]	NA
		X		567.89[2]	NA
DEE~occupancy status		X		**2545.54**	0
	X			2451.20[2]	NA
			X	2454.54[2]	NA
	X	X		2460.54[2]	NA
Proportion of DEE in flight~occupancy status	X			**−812.71**	0
		X		NA	NA
	X	X		NA	NA
			X	NA	NA
Proportion of time in flight~occupancy status	X			**−1367.07**	0
		X		NA	NA
	X	X		NA	NA
			X	NA	NA
Proportion of DEE foraging~occupancy status	X			**−385.81**	0
		X		NA	NA
	X	X		NA	NA
			X	NA	NA

Table A6 (*continued*)

Fixed effect structure	Random effect structure			AIC	ΔAIC
	Intercept	Slope	Combined intercept+slope		
Proportion of time foraging~occupancy status	**X**			**−504.66**	**0**
		X		NA	NA
	X	X		NA	NA
			X	NA	NA
Proportion of DEE active on water~occupancy status	**X**			−531.90	0
		X		NA	NA
	X	X		NA	NA
			X	NA	NA
Proportion of time active on water~occupancy status	**X**			−1033.23	0
		X		NA	NA
	X	X		NA	NA
			X	NA	NA
Proportion of DEE inactive on water~occupancy status	**X**			−160.93	0
		X		NA	NA
	X	X		NA	NA
			X	NA	NA
Proportion of time inactive on water~occupancy status	**X**			−84.59	0
		X		NA	NA
	X	X		NA	NA
			X	NA	NA
Time in flight~Time in occupancy			X	−567.91	0
	X			**−567.43**	**0.48**
	X	X		−548.63	19.28
		X		NA[2]	NA
Time foraging~Time in occupancy		X		−308.48	0
	X			**−309.00**	**0.52**
			X	NA[2]	NA
	X	X		NA[2]	NA

The most supported model with the simplest model structure is shown in bold. NA: the model did not converge and no AIC value could be extracted.
[1] The metric used was DIC (deviance information criterion) not AIC.
[2] The model did not converge.

Table A7
Outputs from LMMs assessing the effect of sex and season on occupancy measures

Response variable	Fixed effects:	Estimate	SE	95% confidence interval
Departure date	**Intercept**	**198.42**	**2.73**	**193.18, 203.90**
	Sex (male)	**−8.26**	**3.32**	**−15.01, −1.81**
	Season (2019−2020)	−3.06	2.28	−7.41, 2.22
	Season (2020−2021)	−4.97	2.97	−10.60, 2.40
	Marginal R^2=0.27, conditional R^2=0.62, N=34 observations			
Log (Moult period duration)	**Intercept**	**95.75**	**9.08**	**78.32, 112.96**
	Sex (male)	18.43	10.57	−1.97, 38.83
	Season (2019−2020)	−1.16	9.34	−19.24, 17.09
	Season (2020−2021)	−8.34	12.01	−31.66, 14.68
	Marginal R^2=0.11, conditional R^2=0.32, N=34 observations			
Return date	**Intercept**	**293.97**	**8.78**	**277.19, 310.62**
	Sex (male)	10.54	10.14	−9.19, 30.02
	Season (2019−2020)	−3.80	9.27	−21.68, 14.54
	Season (2020−2021)	−12.46	11.89	−35.30, 10.61
	Marginal R^2=0.06, conditional R^2=0.24, N=34 observations			
Frequency of absences	**Intercept**	**76.22**	**9.33**	**58.30, 94.57**
	Sex (male)	−6.50	11.65	−29.35, 16.17
	Season (2019−2020)	−5.14	5.82	−16.14, 7.40
	Season (2020−2021)	**−18.02**	**7.38**	**−33.07, −3.93**
	Marginal R^2=0.08, conditional R^2=0.75, N=33 observations			
Duration of absences	**Intercept**	**1.39**	**0.21**	**1.00, 1.80**
	Sex (male)	0.15	0.26	−0.36, 0.66
	Season (2019−2020)	−0.17	0.12	−0.40, 0.07
	Season (2020−2021)	**−0.45**	**0.15**	**−0.75, −0.17**
	Marginal R^2=0.02, conditional R^2=0.23, N=386 observations			
Frequency of presences	**Intercept**	**27.59**	**5.94**	**16.10, 39.00**
	Sex (male)	−8.39	7.34	−22.60, 5.87
	Season (2019−2020)	5.20	4.37	−3.39, 13.58
	Season (2020−2021)	**34.71**	**5.56**	**24.18, 46.24**
	Marginal R^2=0.39, conditional R^2=0.77, N=33 observations			
Duration of presences	**Intercept**	**0.48**	**0.10**	**0.29, 0.68**
	Sex (male)	−0.08	0.13	−0.32, 0.17
	Season (2019−2020)	0.11	0.09	−0.06, 0.28
	Season (2020−2021)	**0.50**	**0.11**	**0.29, 0.72**
	Marginal R^2=0.06, conditional R^2=0.13, N=392 observations			

Significant effects, i.e. those not overlapping zero, are in bold. Reference levels were 'female' for 'Sex' and '2018−2019' for 'Season'.

Table A8
Outputs from an LMM assessing the effect of period, occupancy status and season on the distance from the colony

Fixed effects	Estimate	SE	95% confidence interval
Intercept	**211.54**	**19.30**	**172.78, 182.89**
Period			
Occupancy (absent)	**102.16**	**34.70**	**32.58, 171.96**
Occupancy (present)	**88.34**	**26.24**	**36.11, 141.45**
Season			
2019−2020	**−14.75**	**7.36**	**−29.11, −0.35**
2020−2021	**−21.55**	**10.96**	**−43.07, −0.03**
Period*season			
Occupancy (absent)*2019−2020	**−47.13**	**9.68**	**−66.17, −28.19**
Occupancy (absent)*2020−2021	**−85.13**	**11.81**	**−108.21, −61.83**
Occupancy (present)*2019−2020	13.61	14.29	−14.53, 41.55
Occupancy (present)*2020−2021	**−51.62**	**14.88**	**−80.76, −22.16**
Marginal R^2=0.05, conditional R^2=0.30, N=11 176 observations, 18 groups			

Significant effects, i.e. those not overlapping zero, are in bold. Reference levels were 'moult' for 'Period' and '2018−2019' for 'Season'.

Table A9
LMM R^2 values assessing the effect of occupancy on the proportion of individual daily energy expenditure (DEE) and time (min) to different behaviours

Behaviour	Quantity	Marginal R^2	Conditional R^2 R^2
Foraging	**DEE**	**0.002**	**0.99**
	Time	**0.07**	**0.89**
Flight	**DEE**	**0.60**	**0.98**
	Time	**0.65**	**0.95**
Active	DEE	0.03	0.99
	Time	0.02	0.99
Inactive	DEE	0.003	0.99
	Time	0.0001	0.98

R^2 values from models where a significant difference in the quantity (DEE or Time) was found are highlighted in bold. N = 167 observations for each behaviour.
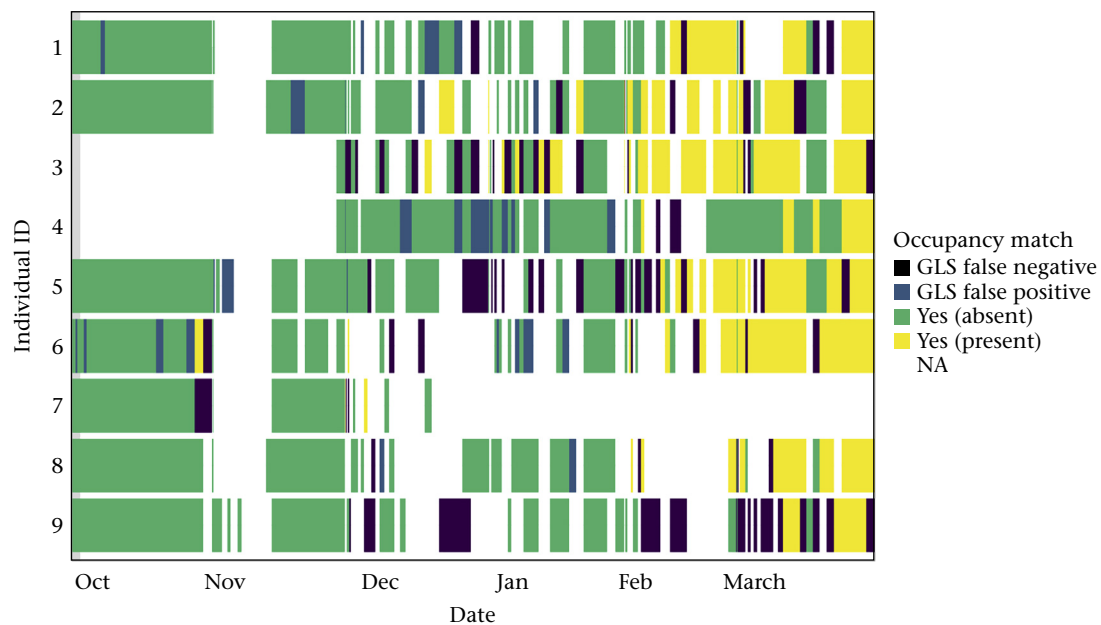
Figure A1. A comparison of camera and geolocator-derived nonbreeding site occupancy for nine individual guillemots from October 2018 to March 2019. 'GLS false negative' were cases when the geolocator determined an individual as 'absent' when the camera determined the individual as 'present'. 'GLS false positive' were cases when the geolocator determined an individual as 'present' when the camera determined the individual as 'absent'.
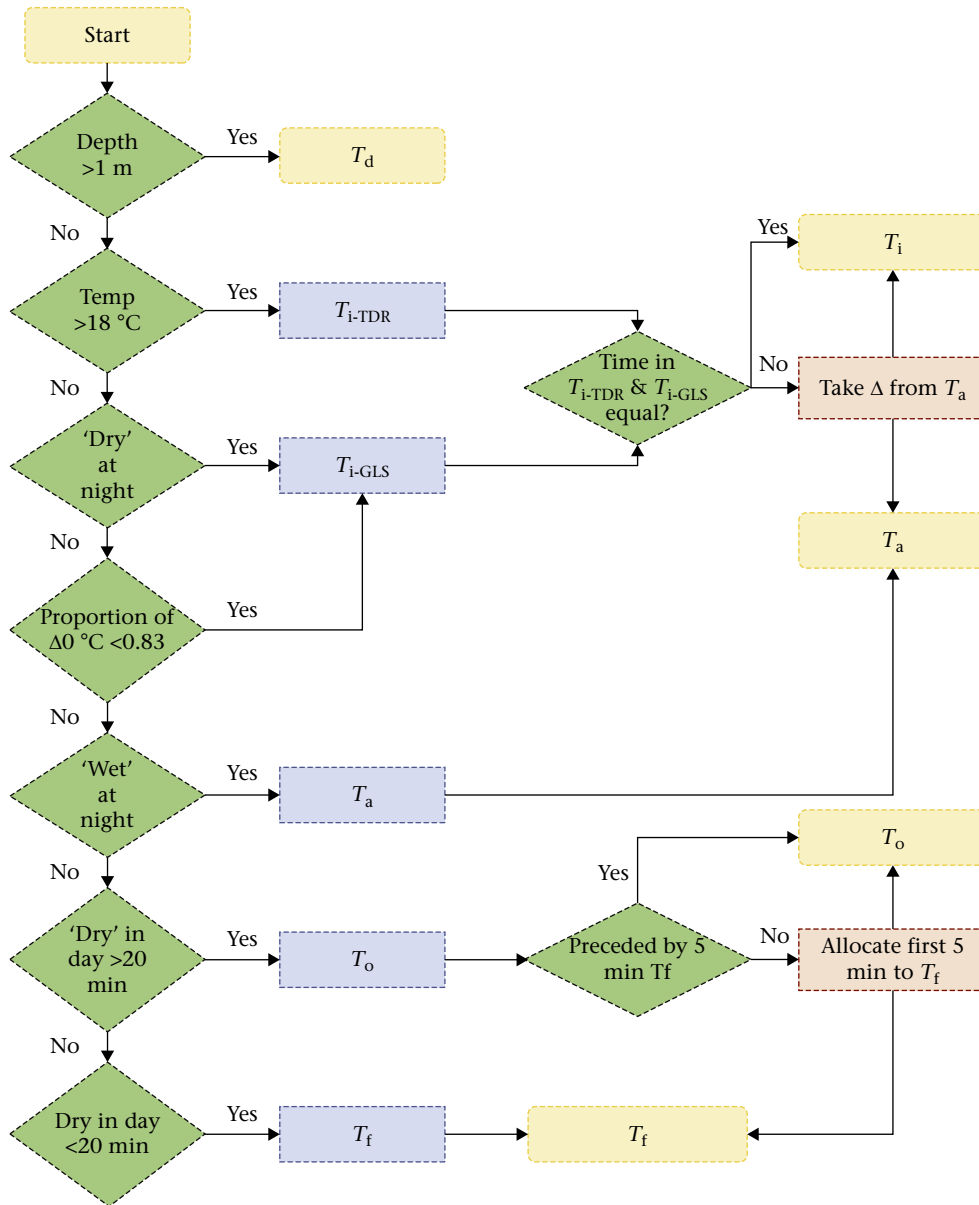
Figure A2. The decision tree process to assign logger activity data to behaviours. Amended from Buckingham et al. (2023).
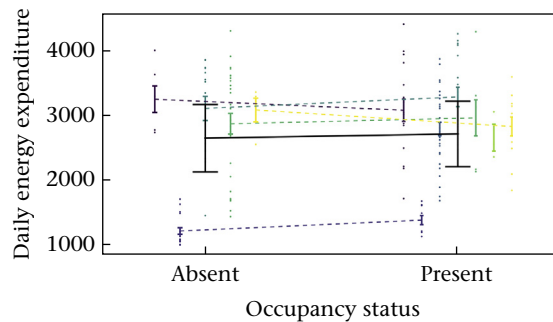

Figure A3. LMM model predictions of daily energy expenditure (kJ) derived using a constant sea surface temperature for individuals on days when an individual was present at or absent from the colony on a given day during the occupancy period. Data are indicated by points and LMM predictions ± 95% confidence intervals by a fitted line and error bars, respectively. Model predictions are in black; other colours indicate individual ID. Group means are joined by dashed lines and are jittered to ease interpretation. $N = 167$ observations and 7 groups.
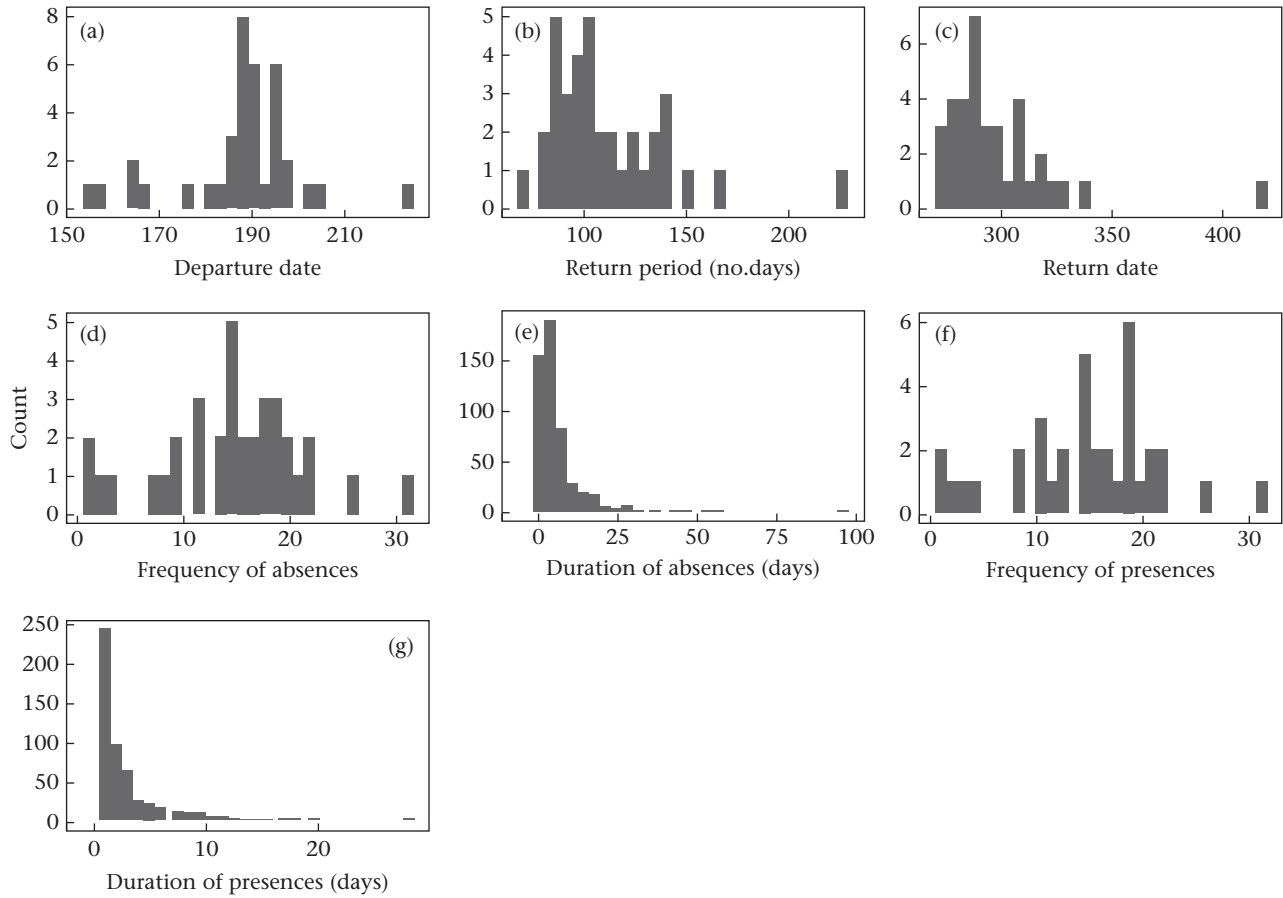
Figure A4. Histograms of individual occupancy measures. (a) Departure date, (b) return period, (c) return date, (d) frequency of absences, (e) duration of absences, frequency of presences and (g) duration of presences. All dates are ordinal. $N = 37$ observations for (a)–(c), and 35 observations for (d)–(g).
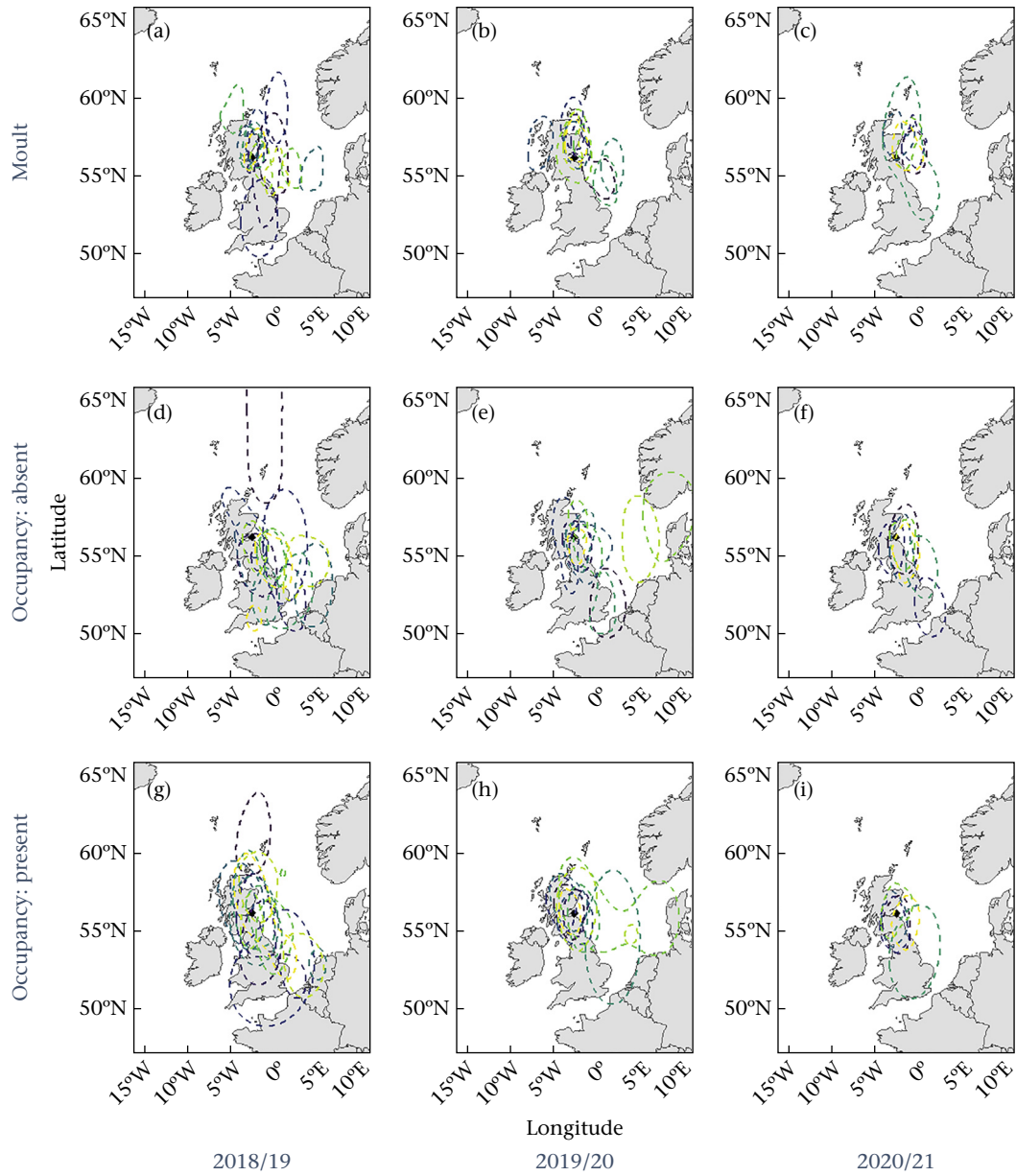
Figure A5. The 50% kernel distributions of individuals in three nonbreeding seasons, (a), (b), (c) during the moult and during the occupancy period on days when individuals were (d), (e), (f) absent or (g), (h), (i) present. Colours indicate individual ID. *N* = 17, 14 and 6 individuals, respectively, for each season.