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Under the cover of darkness: Foraging behaviour increases on cloudy, new moon nights in a pelagic seabird

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While many visual predators feed exclusively during the day, others exploit foraging opportunities at night, although the efficiency with which they do so is strongly influenced by ambient light levels. We investigated the influence of variation in nocturnal light on the foraging behaviour of a small pelagic seabird, the European Storm-petrel *Hydrobates pelagicus*. Nocturnal foraging, identified using GPS-accelerometry data and a Hidden Markov Model, was concentrated in two areas: shallow coastal waters near the colony and deeper offshore waters near the shelf edge. Generalized additive models revealed that, in offshore areas, European Storm-petrels forage under the darkest nocturnal conditions, contrasting with the increased activity under moonlit conditions reported for many other nocturnally foraging seabirds. This was strongly influenced by cloud cover and suggests that European Storm-petrels may be exploiting vertically migrating prey that are more accessible under low ambient light. While olfaction probably plays an important role in detecting prey patches at night, bioluminescence may aid visual detection of individual prey items. In contrast, nearshore foraging was unrelated to nocturnal light and was instead associated with local productivity indicators. If the trend of declining cloud cover in the North Atlantic continues, reducing the frequency of dark nights, European Storm-petrels may alter their nocturnal foraging strategies, forcing them to rely primarily on coastal regions. Our results support growing evidence for the idea that climate-driven and anthropogenic changes to sensory environments are likely to alter the foraging ecology of nocturnal species.

Keywords: climate change, diel vertical migration, nocturnal behaviour, plankton, Procellariiformes.

Climate change has affected multiple facets of animal biology, including physiology (Bozinovic & Pörtner 2015), distribution (Wrensford *et al.* 2025), biomechanics (Domenici & Seebacher 2020), personality (Frost *et al.* 2013) and behaviours, such as migration (Seebacher & Post 2015) and foraging (Evans & Moustakas 2018). However, one comparatively understudied consequence of climate and anthropogenic change is the alteration of animals' sensory landscapes. Anthropogenic sensory pollutants (e.g. artificial light, noise and chemical pollutants), as well as climate-driven changes in environmental cues, can mask critical information, distract individuals or generate misleading signals, thereby disrupting perception and decision-making (Dominoni *et al.* 2020). Consequently, identifying the environmental cues and conditions that species rely on to guide behaviour and decision-making is essential for predicting how they may be affected by future climatic and anthropogenic changes.

Light availability, whether from natural or artificial sources, shapes the nocturnal activity of many species (Fernandez-Duque & Erkert 2006, Prugh & Golden 2014, Nordberg & Schwarzkopf 2022). Chronobiological research has increasingly explored

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how cyclic changes in moonlight act as an environmental cue, regulating behavioural rhythms and potentially influencing underlying biological clocks across a wide range of species (Kronfeld-Schor *et al.* 2013). Brighter full-moon nights often enhance foraging activity in visually orientated predators (Lillywhite & Brischoux 2012, Dwyer *et al.* 2013), while prey species may reduce or alter their movements to minimize the risk of predation (Palmer *et al.* 2017, Farnworth *et al.* 2018). The lunar cycle, therefore, plays a key role in modulating predator–prey dynamics and nocturnal activity patterns.

In marine ecosystems, the ecological consequences of lunar illumination are further complicated by the diel vertical migration (DVM) of zooplankton and small fish. These DVM-performing species typically remain in deeper, darker waters during daylight hours to avoid visual predators in the epipelagic zone, ascending to surface waters at night to feed on phytoplankton (Hays 2003). This nocturnal migration can make them temporarily accessible to surface-feeding or shallow-diving marine predators but the extent of DVM is modulated by ambient light levels. During bright full moon nights, vertically migrating prey may not ascend as close to the surface (Tarling *et al.* 1999, Benoit-Bird *et al.* 2009), presenting visual marine predators with a trade-off between enhanced prey detectability under brighter conditions and reduced prey accessibility. While DVM is most pronounced in deeper offshore waters where distinct isolumes (depth layers receiving the same light intensity) exist, it also occurs in coastal areas. In these shallower regions, however, high turbidity can restrict light penetration, resulting in some DVM planktonic species remaining near the surface regardless of light conditions (Ens *et al.* 2024). Coastal DVM patterns therefore may be driven by factors in addition to light, such as tidal currents (Ollevier *et al.* 2024).

Most seabird species rely heavily on visual cues when foraging (Martin & Prince 2001), and consequently, light availability influences both diurnal and nocturnal foraging behaviour (e.g. Yamamoto *et al.* 2008, Darby *et al.* 2022). While many species show limited nocturnal activity under low-light conditions (Wanless *et al.* 1990, Harris *et al.* 2012, Dean *et al.* 2013, Bennison *et al.* 2019), others exploit foraging opportunities enabled by moonlight (Regular *et al.* 2011, Elliott & Gaston 2015). Nocturnal foraging has been observed in several Procellariiformes, with peak activity often associated with higher lunar light intensities (Phalan *et al.* 2007, Dias *et al.* 2012, Rubolini *et al.* 2015, Ramos *et al.* 2016). Paradoxically, DVM mesopelagic prey are typically further from the surface on brighter nights (Tarling *et al.* 1999, Benoit-Bird *et al.* 2009), so the association between nocturnal foraging behaviour and higher lunar light intensity is likely to be due to birds targeting epipelagic species that are relatively more visible under bright moonlight.

In addition to the cyclical changes in moonlight, cloud cover plays a key role in shaping nocturnal illumination (Jechow *et al.* 2019). Dense cloud cover can substantially diminish ambient light regardless of moon phase, potentially altering visual detection conditions and influencing predation risk for nocturnally active species (Prugh & Golden 2014). In marine systems, cloud cover can influence the amplitude of DVM in prey species by altering underwater light conditions (Omand *et al.* 2021, Bandara *et al.* 2022), thereby shifting their vertical distribution higher in the water column and improving their accessibility to surface-feeding predators.

The European Storm-petrel *Hydrobates pelagicus* provides an ideal model for examining these relationships. The species' foraging habitat preferences are shaped by bathymetric and physical oceanographic features (Scott *et al.* 2013, De Pascalis *et al.* 2021, Bolumar Roda *et al.* 2025), and its diet in the North Atlantic primarily comprises zooplankton (e.g. Cnidaria, Ostracoda, Copepoda and Euphausiacea) and small fishes, including DVM-performing species, captured at the sea surface (D'Elbée & Hémery 1998). European Storm-petrels are highly active at sea both during the day and at night (De Pascalis *et al.* 2025, Wilkinson *et al.* 2026), and nocturnal foraging has been observed (Thomas *et al.* 2006, Albores-Barajas *et al.* 2011). However, it remains unclear whether moonlight facilitates nocturnal foraging by enhancing visual detection of prey, or instead inhibits foraging by reducing the availability of surface prey on brighter nights.

In this study, we investigate how nocturnal foraging behaviour in European Storm-petrels varies with ambient light conditions, considering both moonlight and cloud cover. Specifically, we test the competing hypotheses that increasing moonlight either promotes nocturnal foraging by improving the visual detection of prey or constrains

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foraging by reducing the availability of vertically migrating prey near the sea surface. By identifying how natural variation in the nocturnal light environment influences foraging behaviour, our study provides new insight into the sensory ecology of a pelagic seabird and establishes a foundation for understanding how future environmental change may affect predator–prey interactions in marine ecosystems.

METHODS

Data collection

Breeding European Storm-petrels from two colonies were deployed with Pathtrack nanoFix Geo-Mini (<1 g) GPS tags over the course of four breeding seasons. In 2016, 11 devices were deployed at High Island, Co. Galway, Ireland (53.546 N, −10.258 W). A further 24 tags were deployed at Illauntannig, Magharee Islands, Co. Kerry, Ireland (52.326 N, −10.022 W), during the 2020 (n = 6), 2023 (n = 5) and 2024 (n = 13) breeding seasons. All tags were programmed to record locations in 30-min intervals except four tags deployed in 2024, which were set to have a 15-min resolution and included tri-axial accelerometers that recorded data continuously at 25 Hz with sensitivity up to ±8 g. The body mass of each Storm-petrel was recorded before deployment and after removing the GPS device. In all years, the GPS tags were attached to the four central tail feathers using Tesa tape. The total deployment weight represented 3.48 ± 0.27% of the birds' body mass, and tags were deployed with the aim of being retrieved after a single foraging trip. No significant difference in body mass was recorded after tag retrieval (Appendix S1).

Identifying at-sea behaviours

All foraging trips were split into three behavioural states (transiting, foraging and resting) following the methodology outlined in Wilkinson *et al.* (2026). First, a two-state Hidden Markov Model (HMM) was applied to all GPS data, interpolated to 30-min intervals, to distinguish between transiting and foraging behaviour. The coarse temporal resolution of the GPS data prevented resting behaviour from being distinguished from foraging. Secondly, accelerometer-derived standard deviation of overall dynamic body acceleration (ODBA) was used to differentiate low-activity resting from high-activity flying in the tracks that had accelerometer data. This allowed the tracks that had both GPS and accelerometer data to be separated into three behaviours, and to correct any points mis-identified as foraging by the two-state HMM that in reality were resting. Thirdly, the confirmed behaviour for each point within these GPS-accelerometry tracks was used to produce a semi-supervised three-state HMM of all GPS data using the *knownStates* argument within the 'fitHMM' function from the *momentuHMM* package (McClintock & Michelot 2018). This enabled the model to learn the characteristic movement signatures (step lengths and turning angles) linked to each behaviour in the GPS-accelerometry tracks and subsequently apply these learned patterns to classify behaviours in the remaining GPS-only tracks. Starting parameters were selected by evaluating the log-likelihood values of 50 candidate models using random priors for step length and turning angle concentration from a range of reasonable values (De Pascalis *et al.* 2021). A gamma distribution for step length and a Von Mises distribution with a mean of zero for turning angle were used for all candidate models, and the sequence of behaviours was defined using the Viterbi algorithm. This approach enabled classification of all GPS tracks into three behavioural states, including those lacking accelerometer data (see Wilkinson *et al.* (2026) for more information). The proportion of time individuals spent in each behaviour state was compared between day and night using a Wilcoxon signed-rank test, with night defined as the period between evening and morning civil twilight, and the timings were calculated using the *suncalc* package (Thieurmel & Elmarhraoui 2022). All analyses were conducted using R version 4.5.1 (R Core Team 2025).

Explanatory variables of nocturnal foraging

Only GPS data points that occurred at night were retained for this analysis. Environmental variables hypothesized to influence European Storm-petrel nocturnal foraging behaviour were appended to each night-time GPS point. Spatial variables, including distance to the coast, distance to the 500 m isobath (representing the continental shelf edge) and seabed depth, were calculated using the *marmap* package (Pante *et al.* 2023). The *raster* package (Hijmans 2023) was used to derive seabed

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slope and the distance of each point to the breeding colony while avoiding land. Chlorophyll *a* concentration (chl-*a*; mg m^{-3}) and sea surface temperature (SST; °C) are dynamic environmental variables associated with marine productivity that are commonly used to model the distribution of seabird foraging behaviour (e.g. Tremblay *et al.* 2009, Kane *et al.* 2020, Serratosa *et al.* 2020). These terms were obtained at 8-day temporal and 4 km spatial resolution from Movebank's Env-Data service (Dodge *et al.* 2013) which uses NASA's MODIS satellite data. Eddy kinetic energy (EKE; m^2 s^{-2}), a proxy for mesoscale eddies that have been identified as important features for European Storm-petrel foraging (De Pascalis *et al.* 2021, Bolumar Roda *et al.* 2025), was calculated as EKE = ½ $(u^2 + v^2)$ using zonal (u) and meridional (v) water velocity. These measures of water velocity were sourced from the Copernicus Marine Environment Monitoring Service (marine.copernicus.eu) at daily 0.083° resolution. Time relative to sunset (end of evening civil twilight) was calculated and the *suncalc* package (Thieurmel & Elmarhraoui 2022) was used to source the illuminated fraction of the moon, which varies from 0.0 (new moon) to 1.0 (full moon). As the effect of moonlight is influenced by cloud cover, cloud coverage data were sourced from the European Centre for Medium-Range Weather Forecasts' ERA5 datasets (climate.copernicus.eu) at hourly 0.25° resolution.

Modelling the drivers of nocturnal foraging

Nocturnal foraging occurred in two distinct regions (Fig. 1): shallow waters near the colony and deeper offshore waters, which were visited during multi-day foraging trips. To account for these differences, the dataset was divided into shallow nearshore (<100 m depth) and deeper offshore (>100 m depth) subsets, with separate models fitted for each. Modelling each region separately was selected to simplify the modelling process and to avoid correlation issues where terms were correlated in one region but not the other.

The 100 m depth contour was selected as the boundary between nearshore and offshore waters because the Irish Coastal Current, which originates off western France and transports phytoplankton, zooplankton and nutrients into coastal regions of southern and western Ireland, typically flows in waters shallower than 100 m during the summer months (Fernand *et al.* 2006, Farrell *et al.* 2012, McGuinness *et al.* 2025). In addition, the seabed slopes steeply between the 80 and 100 m contours before extending towards the shelf edge as a relatively flat platform, indicating a marked transition in seabed topography at 100 m depth (Fernand *et al.* 2006, Ren *et al.* 2023). Beyond the 100 m contour, prey abundance and availability are influenced by oceanographic features, such as the Irish Shelf Front (Huang *et al.* 1991, McMahon *et al.* 1995), and shelf-edge upwelling, which drive the influx of nutrient-rich waters that support high plankton productivity (Raine *et al.* 1990) and, consequently, enhance prey availability for foraging Storm-petrels.

In both models, the presence or absence of foraging at each nocturnal tracking point was modelled as a function of a set of covariates using a binomial generalized additive mixed model (GAMM) with a logit link function. The 'bam' function from the *mgcv* package (Wood 2011) was used because it supports the inclusion of a first-order autoregressive (AR1) correlation structure. This accounts for temporal autocorrelation in the data by incorporating a coefficient (rho), estimated using an autocorrelation function, which quantifies the serial correlation between consecutive tracking points. All covariates were included in both models, except for distance to the colony, which only featured in the nearshore model, and distance to the continental shelf edge, which was only included in the offshore model. A bi-dimensional tensor spline of moon fraction and cloud cover was included in both models to account for their combined influence on lunar light levels. Individual ID was included as a random effect, and all other covariates were fitted using penalized thin-plate regression splines with shrinkage to avoid overfitting. The gamma parameter was set to 1.2, which increases the null space penalty (Wood 2003), to further reduce model complexity. Where required, variables were transformed using a Box-Cox transformation to improve normality prior to model fitting (Table S1).

Highly correlated covariates were identified using the 'concurvity' function in *mgcv* and removed stepwise. A high threshold of 0.8 was used, consistent with other seabird studies (e.g. Darby *et al.* 2021), to avoid masking partial effects of related variables. Model selection was facilitated by introducing an additional penalty to model

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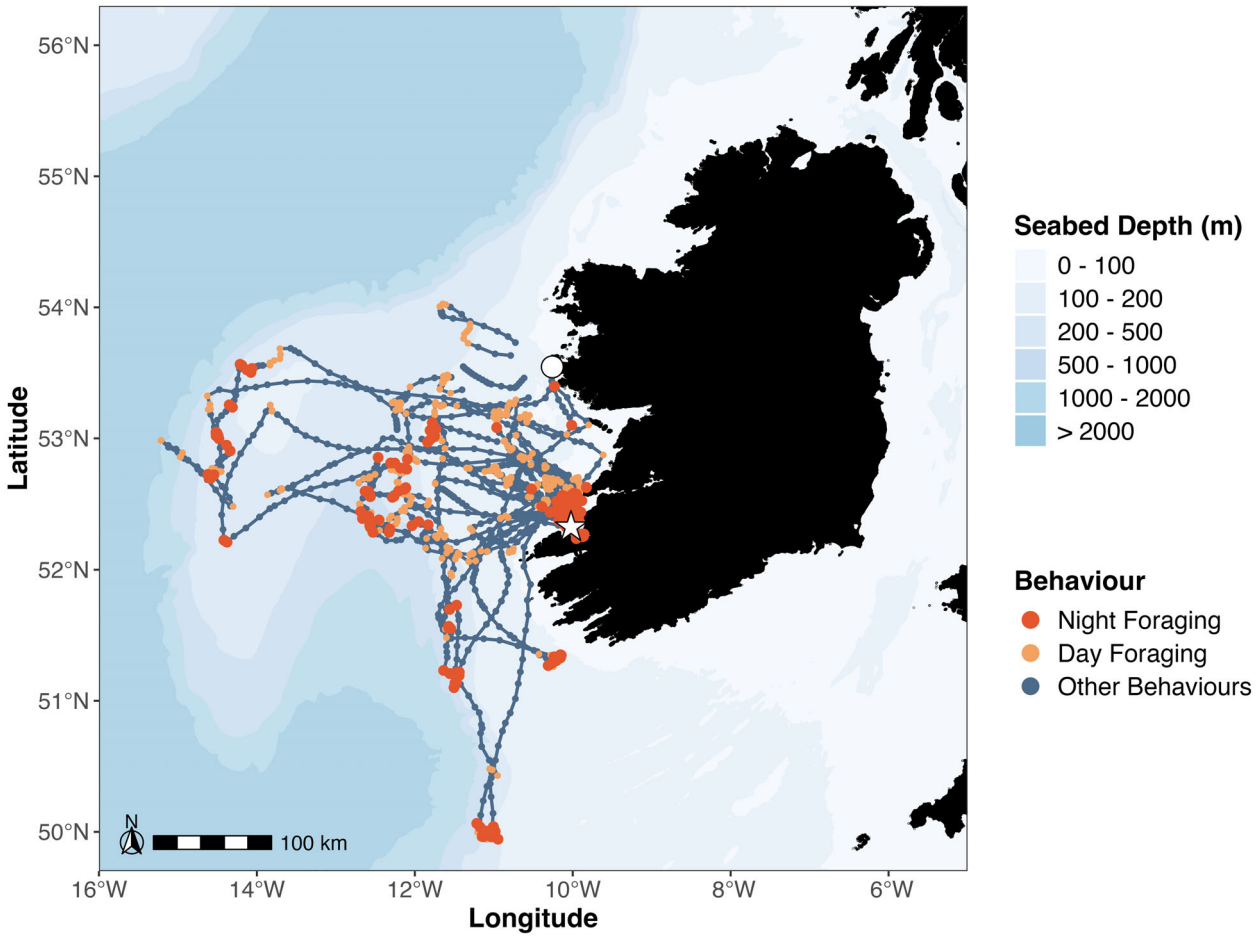

Figure 1. GPS tracks of foraging trips conducted by breeding European Storm-petrels showing night-time and daytime foraging points. White circle = High Island; white star = Illauntannig, Magharee Islands. The shaded blue areas represent the 100, 200, 500, 1000 and 2000 m bathymetric contours.

terms with smoothing parameters approaching zero. This feature within *mgcv* drives the effect of non-contributing covariates to zero, functionally excluding them from the model (Wood 2011). Model goodness-of-fit was described using deviance explained.

RESULTS

Tag retrieval

Across the four breeding seasons, 21 GPS devices were recovered, although retrieval rates varied between years (Appendix S2). Four devices experienced technical issues that prevented GPS locations from being recorded for most of the trips and were therefore excluded from further analysis. Most of the 17 remaining devices recorded a single trip; however, two tags deployed at the Magharee Islands colony recorded two complete trips each because the tagged Storm-petrels were not recaptured on their first return to the colony. The final dataset consisted of 11 complete and eight incomplete trips. Of the incomplete trips, two were close to complete, only missing a few hours of data, but the remaining sections of incomplete trips were composed of between 8.5 and 20 h of GPS data.

At-sea behaviour of European storm-petrels

Most of each complete or near-complete foraging trip was performed during daylight hours

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(mean = 73%, range = 63–89%, n = 13). Of the 1015 daytime locations from these trips, 431 (42.5%) were foraging, 137 (13.5%) were resting and 447 (44.0%) were transiting. At night, Storm-petrels spent 93.6% of the time flying, split between 209 (53.9%) foraging and 154 (39.7%) transiting locations, leaving just 25 (6.4%) of the night-time locations allocated to resting. There were no statistical differences between day and night in the proportions of time individuals spent foraging (W = 25, P = 0.168) or transiting (W = 54, P = 0.588). However, resting occurred more during the day than at night (W = 65, P = 0.045). During daylight hours, most activity occurred in offshore waters (>100 m depth), with only 30% of foraging locations occurring near the coast (Table 1). At night, however, foraging was more evenly distributed between offshore and nearshore areas, with slightly more foraging activity nearshore (Table 1).

Individual-level random effects were initially included in both offshore and nearshore models. However, because most individuals contributed only a single foraging trip, there was insufficient replication to estimate individual variation reliably. In the offshore model, the estimated variance of the random effect was effectively zero and the term was heavily penalized during model fitting. In the nearshore model, the random effect exhibited high concurvity (high correlation) with other model terms and was therefore omitted from the final model. In the offshore foraging probability GAM, seabed depth and distance to the shelf edge were removed due to concurvity with other covariates. In addition, the effects of SST and EKE were reduced to zero. Time of night was retained in the final model but its effect was non-significant (Table S2). The probability of nocturnal foraging offshore increased with greater distance from the coast (Fig. 2a) and steeper seabed slopes (Fig. 2b), while the relationship with chl-*a* was non-linear but showed the greatest probability at higher concentrations (Fig. 2c). Storm-petrels also foraged more under darker conditions, with higher foraging probabilities during new moon phases and heavy cloud cover (Fig. 2d). The model explained 20.4% of the deviance.

Seabed depth and SST were removed from the nearshore foraging probability model due to concurvity, while the effects of EKE, distance to the coast, and the tensor interaction between moon fraction and cloud cover were reduced to zero. The final model explained 15.6% of the deviance and showed that nocturnal foraging probability in nearshore areas was highest in regions with elevated chl-*a* (Fig. 3a) and steep seabed slopes (Fig. 3b). The relationship with distance to the colony was not significant (Table S3) but showed higher foraging probability close to the colony. Foraging activity declined over the course of the night (Fig. 3c).

DISCUSSION

Patterns of nocturnal foraging in animals are often tightly linked to ambient light levels, with many species increasing activity under brighter lunar conditions that enhance visual detection of predators or prey, as demonstrated across a range of taxa, including terrestrial mammals (Brivio *et al.* 2017, 2024, Ladine & Settles 2020), reptiles (Lillywhite & Brischoux 2012) and seabirds (Phalan *et al.* 2007, Regular *et al.* 2011, Rubolini *et al.* 2015, Ramos *et al.* 2016). In contrast, our results demonstrate that some marine predators exhibit peak foraging activity under the darkest conditions, highlighting alternative sensory strategies. The similar allocation of foraging effort across day and night observed in

Table 1. Number of European Storm-petrel GPS points (*N*) classified as foraging, resting and transiting during the day and night, and the breakdown between offshore and nearshore areas.

	Day			Night		
	N	Offshore	Nearshore	*N*	Offshore	Nearshore
Foraging	431	302 (70%)	129 (30%)	209	99 (47%)	110 (53%)
Resting	137	108 (79%)	29 (21%)	25	16 (64%)	9 (36%)
Transiting	447	376 (84%)	71 (16%)	154	85 (55%)	69 (45%)
All Points	1015	786 (77%)	229 (23%)	388	200 (52%)	188 (48%)

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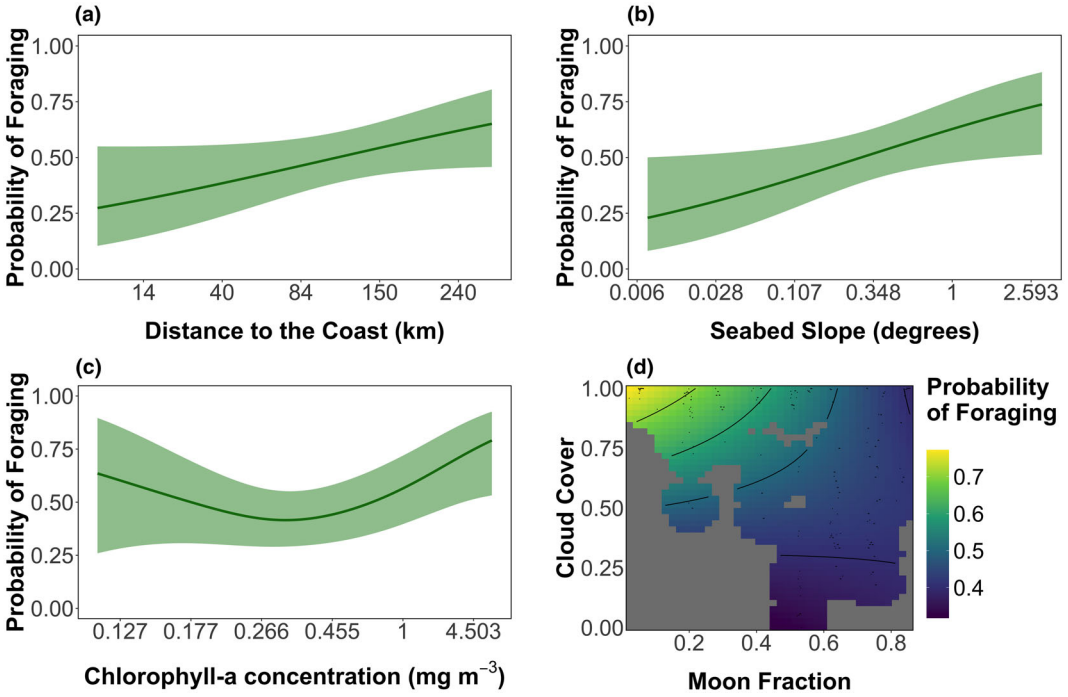

Figure 2. Significant generalized additive model (GAM) covariates describing the probability of nocturnal foraging of European Storm-petrels in offshore areas. Shaded areas in (a)-(c) represent the 95% confidence intervals. Grey areas in (d) indicate no available data.

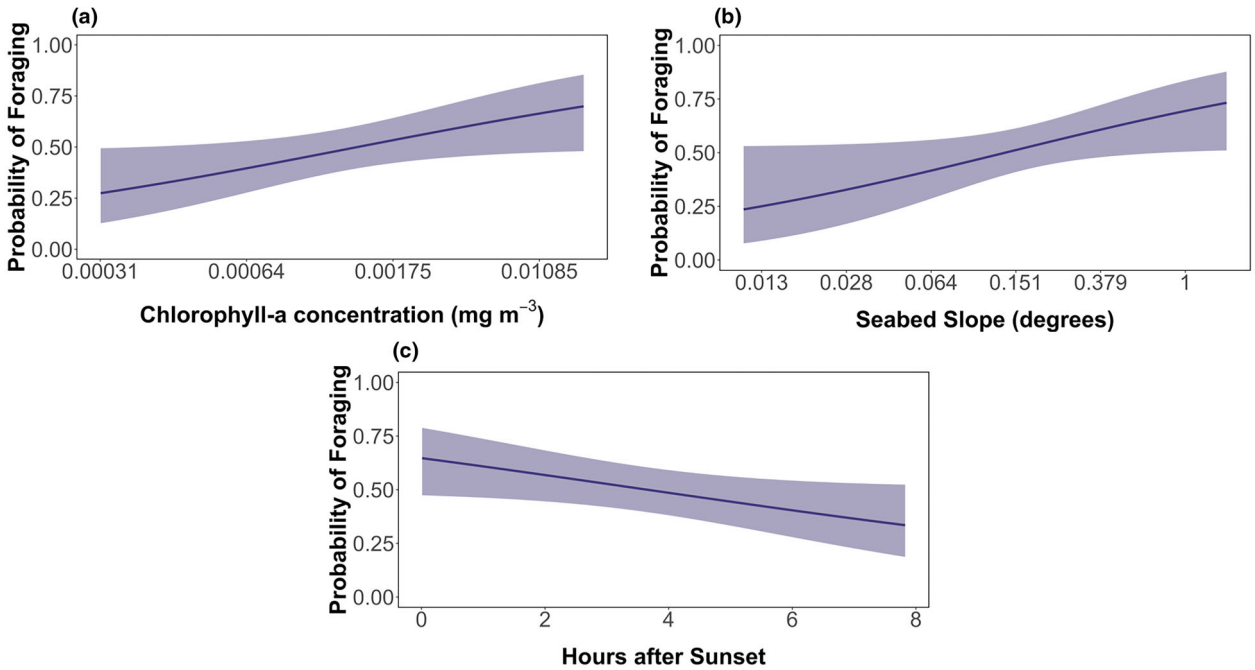

Figure 3. Significant generalized additive model (GAM) covariates describing the probability of nocturnal foraging of European Storm-petrels in shallow, nearshore areas. Shaded areas represent the 95% confidence intervals.

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the European Storm-petrel suggests a high degree of behavioural flexibility in response to variable light environments, challenging the assumption that nocturnal foraging in many seabird species is predominantly light-facilitated (e.g. Regular *et al.* 2011, Elliott & Gaston 2015, Ostaszewska *et al.* 2017). To our knowledge, the preference of darker conditions for nocturnal foraging has only been described in one other seabird species, the Swallow-tailed Gull *Creagrus furcatus*, which forages exclusively at night in the South Pacific (Cruz *et al.* 2013) and possesses ocular adaptations for enhanced light sensitivity (Iwaniuk *et al.* 2010). Consequently, our findings raise the question of how European Storm-petrels detect and capture small prey items at the sea surface under such low-visibility conditions.

A likely explanation is that European Storm-petrels rely on multiple sensory cues operating at different spatial scales. Like other Procellariiformes, European Storm-petrels possess a well-developed olfactory system and can use scents to locate prey patches (Nevitt *et al.* 2004, Humphries *et al.* 2012). Odours released by phytoplankton can trace bathymetric features, such as the shelf edge, creating an 'olfactory landscape' that guides Storm-petrels to productive offshore habitats (Nevitt 2008) potentially assisted by prevailing wind conditions (Ventura *et al.* 2022, De Pascalis *et al.* 2026). In our study, increased foraging in high chl-*a* areas and over steep seabed slopes at greater distances from the coast supports this link with bathymetry and olfaction. However, while olfactory cues probably direct Storm-petrels to prey patches, it remains unclear whether smell alone enables detection of individual prey items on the sea surface, or if visual cues are also required, as observed in other Procellariiformes (Martin & Brooke 1991, Martin & Prince 2001, Nevitt *et al.* 2008). The European Storm-petrel eye exhibits several adaptations for low-light vision compared with similarly sized diurnal birds, including elongated photoreceptor outer segments and a thick outer plexiform layer (Pollard 2009), which may facilitate nocturnal prey detection.

The increased probability of foraging on darker nights suggests that nocturnal foraging in European Storm-petrels is closely linked to enhanced prey availability resulting from DVM, as has been identified in the Swallow-tailed Gull (Cruz *et al.* 2013). At night, DVM-performing organisms ascend to the surface and mix with resident prey species, increasing overall prey density, enhancing prey encounter rates and making otherwise inaccessible prey available to surface-feeding Storm-petrels. Any ambient light may cause DVM species to remain deeper in the water column (Tarling *et al.* 1999, Benoit-Bird *et al.* 2009) and subsequently beyond their reach. Bioluminescence may provide an additional foraging cue on dark nights. Many mesopelagic species that undertake DVM are bioluminescent and these light-emitting species could serve as visual signals to Storm-petrels in the absence of moonlight. The strong attraction of Storm-petrels to artificial lights on dark nights (Miles *et al.* 2010, Medina-Franco *et al.* 2025) has been interpreted as confusion with bioluminescent cues (Imber 1975). Evidence from other Procellariiformes supports the potential use of bioluminescence for prey detection, with a study examining the timing of ingestion for prey items of different masses concluding that Wandering Albatrosses *Diomedea exulans* probably feed predominantly on non-bioluminescent prey during the day and bioluminescent squid at night (Weimerskirch *et al.* 2005). Other marine predators also rely on bioluminescence for nocturnal foraging (Vacquié-Garcia *et al.* 2012), and importantly, bioluminescent taxa (e.g. *Candacia armata*, *Pareuchaeta norvegica*, *Metridia lucens*, *Nyctiphanes couchii* and Myctophidae) have been recorded in the Storm-petrel diet (D'Elbée & Hémery 1998). Although our study provides no direct evidence that Storm-petrels use bioluminescence during prey capture, these observations support the hypothesis that bioluminescent signals may facilitate prey detection by Storm-petrels in offshore environments during the darkest nights.

In nearshore regions, increased foraging activity was associated with indicators of high productivity (high chl-*a* and steep seabed slope) and showed no effect of moonlight. Chl-*a* is widely used as a proxy for primary productivity and therefore prey availability in the marine environment (Tremblay *et al.* 2009), while the topographic structure of the seabed can influence prey distribution (Cox *et al.* 2018) with steep slopes associated with increased productivity. Near-colony nocturnal foraging has been documented in the Mediterranean during the breeding season, where European Storm-petrels fed on Mysidacea (Albores-Barajas *et al.* 2011). These and related organisms occur in high abundances in our study area (Tully & Ó Céidigh 1987) and as light-modulated DVM tends

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to be less pronounced in highly productive waters near the coast compared with offshore areas (Burt & Tortell 2018), prey in these areas may remain abundant throughout the night regardless of lunar light availability. The prevalence of nocturnal foraging in productive coastal habitats indicates it is a fundamental foraging strategy for European Storm-petrels. Nearshore foraging also declined as the night progressed, probably reflecting a shift from foraging to commuting away from the coast as dawn approached (Wilkinson *et al.* 2026), consistent with predator-avoidance behaviour during the day (Bolton 2021, Wilkinson *et al.* 2025). Offshore, this pattern was absent, supporting the hypothesis that Storm-petrels already far from the coast are not subject to the same predation pressures. Although low SST and high EKE have been linked to European Storm-petrel foraging activity in the Mediterranean (De Pascalis *et al.* 2021, Bolumar Roda *et al.* 2025), neither variable was retained in our models, potentially suggesting different environmental cues are used by Storm-petrels when foraging in the Mediterranean compared with nocturnal foraging in the north-east Atlantic.

These findings have important implications in the context of ongoing climate change. Offshore foraging by European Storm-petrels depends on darkness generated by both lunar phase and cloud cover. However, cloud cover over the Atlantic has declined over the past decade (Goessling *et al.* 2025), a trend with potentially significant consequences for this species and other species with similar reliance on dark conditions for foraging. Reduced cloud cover has been identified as a contributing factor to marine heatwaves, which are increasing in frequency (Oliver *et al.* 2018), including the 2023 North Atlantic marine heatwave (England *et al.* 2025, Goessling *et al.* 2025) that affected the waters of our study area (McCarthy *et al.* 2023). While further reductions in cloud cover may promote additional marine heatwaves, with numerous direct and indirect impacts on seabirds (Piatt *et al.* 2024), a less recognized consequence is the increased frequency of bright nights and the potential disruption of nocturnal foraging in species that rely on darkness, such as the European Storm-petrel in the North-East Atlantic and the Swallow-tailed Gull in the South Pacific (Cruz *et al.* 2013). Brighter nocturnal conditions may cause European Storm-petrels to alter their foraging strategies, potentially shifting prey selection in response to changes in the vertical distribution of DVM prey or reduced detection of bioluminescent cues. Such dietary shifts could increase competition with seabird species that already exploit moonlit conditions for nocturnal foraging. Alternatively, Storm-petrels may relocate nocturnal foraging activity closer to coastal areas, where light levels appear to exert less influence on behaviour, potentially with consequences for energy expenditure and foraging efficiency. These inferences should, however, be interpreted with some caution. Cloud cover was estimated from ERA5 reanalysis products and therefore represents model-derived rather than direct measurements of local atmospheric conditions. In addition, because most individuals were tracked for a single foraging trip, it was not possible to assess consistent individual variation in response to nocturnal light conditions. Nevertheless, the strong relationships observed between nocturnal foraging and ambient light suggest that changes in cloud cover have the potential to influence predator–prey interactions in offshore marine environments.

CONCLUSION

Our study demonstrates that darkness can facilitate rather than constrain nocturnal foraging by surface-feeding seabirds. Consequently, declining cloud cover may reduce nocturnal foraging opportunities for European Storm-petrels and other darkness-dependent species. As some species increasingly adopt nocturnal activity to mitigate heat stress associated with rising daytime temperatures (Levy *et al.* 2019, Rafiq *et al.* 2023, Brivio *et al.* 2024), the prevalence of nocturnality may expand under future climate scenarios. Our findings highlight the critical role of sensory and environmental drivers in shaping nocturnal foraging strategies and underscore the potential vulnerability of darkness-dependent species to climate-driven shifts in cloud cover and nocturnal light regimes.

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AUTHOR CONTRIBUTIONS

Adam Kane: Data curation; investigation; methodology; writing – review and editing. **Darren Wilkinson:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; visualization; writing – original draft; writing – review and editing. **John L. Quinn:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing – review and editing. **Mark Jessopp:** Conceptualization; funding acquisition; investigation; methodology; supervision; writing – review and editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ETHICAL NOTE

All fieldwork was approved by University College Cork's animal ethics committee and licensed by the British Trust for Ornithology and the National Parks and Wildlife Service (C100/2016; 025/2016; 06/2020; C41/2020; C114/2023; 076/2023; C145/2024; and 044/2024).

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DATA AVAILABILITY STATEMENT

GPS data used for this publication are available from the Seabird Tracking Database (https://data.seabirdtracking.org/) (study numbers: 1576 and 2449). All code is freely available at Zenodo (DOI: 10.5281/zenodo.21532347).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Impacts of tagging.

Appendix S2. Tag recovery rates.

Table S1. λ (lambda) values used in the Box-Cox transformation of variables prior to model fitting.

Table S2. GAM terms explaining the probability of nocturnal foraging in offshore areas.

Table S3. GAM terms explaining the probability of nocturnal foraging in nearshore areas.

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