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Evidence for latitude-driven changes in diel rhythms in a wide-ranging seabird

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Diel rhythms synchronized to Earth’s photic cycle are near-ubiquitous among animals living in regions with distinct day–night cues. Where such cues are reduced or absent, however, activity patterns may weaken, reorganize or become decoupled from the light–dark cycle, which may allow for more flexible behavioural expression. Using a dataset of >900 free-ranging black-legged kittiwakes from colonies spanning a broad latitudinal gradient (40–81°N), we show considerable population-level variation in diel activity patterns, from clear 24 h rhythms with distinct peaks at dawn and dusk at lower latitudes, to variable and non-diel rhythms with flattened activity patterns across the 24 h day at high latitudes. These patterns were consistent with the wide spectrum of light–dark cycles experienced across their breeding range, supported by our finding that activity was strongly predicted by sun elevation, suggesting alignment with the light–dark cycle. Together, our findings reveal substantial within-species variation in rhythmicity across latitudes and demonstrate that changes in the photic environment can reshape the temporal organization of activity even within a single, widely distributed species.

1. Introduction

Nearly all animals studied to date have coordinated physiological and behavioural patterns that align to the 24 h day, known as diel rhythms, for at least part of their life cycle [1–5]. For the vast majority of species, these rhythms are synchronized by the Earth's light–dark cycle, which is typically the most consistent, reliable and widely available cue for timing activity [4,6]. At high latitudes, however, seasonal variation in night length weakens this cue, creating conditions under which diel timing cannot rely on a pronounced light–dark cycle. Under such constraints, the mechanisms by which diel rhythms are expressed in wild populations remain poorly resolved. Comparative and population-level studies have revealed substantial diversity in diel rhythms under continuous daylight. In many species, rhythms are maintained using other predictable environmental cues, such as temperature fluctuations, atmospheric conditions or biotic interactions [7–17], either alongside or alternatively to photoperiodic cues [18]. By contrast, other species exhibit weakened or apparently absent diel rhythms [19,20] cf. [21,22] or rely on cues that produce rhythms deviating markedly from 24 h [23–25].

While such interspecific diversity in diel rhythms is well documented [26], comparatively little is known about how rhythmicity varies within species, particularly across populations spanning broad latitudinal ranges. Evidence to date indicates that rhythmicity can vary at multiple biological scales. Even within species, individuals breeding within the same population may differ markedly in the strength or timing of their rhythms [18,27], and comparative studies have documented pronounced differences among species across latitudinal gradients [22,28]. More recently, semi-experimental work within a captive species [29] and across a selection of wild species [30] has demonstrated that rhythmic expression may be modified through exposure to variation in environmental cues. However, it remains unclear whether within-species rhythmicity changes predictably with latitude, and whether rhythms attenuate gradually as environmental cues weaken or cease entirely.

Despite recent advances, most studies of high-latitude chronobiology have focused on single populations, limited latitudinal ranges or short time periods. Consequently, we lack a general understanding of how diel rhythms within species change across latitude. Understanding such patterns requires species that naturally experience a wide range of photic regimes while maintaining similar behavioural constraints. Kittiwakes meet these criteria: as surface-feeding, visually hunting seabirds with a wide latitudinal breeding distribution from *ca* 40°N to 81°N [31–33], spanning light regimes from strict day–night cycles to continuous daylight, they provide a powerful study system for investigating changes in diel rhythms across latitudes. During the breeding season, kittiwakes forage on small fishes and zooplankton on trips to sea that last from only a few hours to a few days, typically resting on the water during multi-day trips [34,35].

We collected unprecedented activity data from >900 free-ranging black-legged kittiwakes *Rissa tridactyla* (hereafter 'kittiwakes') to test how activity patterns vary with latitude, giving insight into both the flexibility and constraints of behavioural timing in continuous daylight. Using tracking data from 24 populations spanning approximately 30° of latitude and multiple years, we tested a series of linked hypotheses concerning the detection, structure, persistence and environmental modulation of diel rhythms in kittiwakes. We hypothesized that increasing exposure to continuous daylight at high latitudes weakens the expression of diel rhythmicity and alters how activity is structured in time. Specifically, we predicted that with increasing latitude: (i) rhythmic expression would become weaker and less temporally consistent as night shortens; (ii) activity patterns would become less tightly aligned with solar cues as these cues become less informative; and (iii) during foraging trips, when birds are freed from colony attendance constraints, activity would become increasingly distributed across the 24 h cycle. Together, these analyses provide a framework for understanding how diel rhythms adapt to varying photic environments within a single species.

2. Methods

We used data collected from the SEATRACK project between 2013 and 2023 [36]. A total of 971 kittiwakes from 24 colonies across the North Atlantic from Canada, Greenland, Iceland, Ireland, Norway, Russia and the United Kingdom were used in the study (figure 1; full details in electronic supplementary material, table S1). All birds were captured on the nest during the breeding season and marked with a stainless-steel metal ring for individual identification. To determine behavioural rhythms, we fitted individuals with Migrate Technology (Cambridge, UK; model numbers: w65, c65, c65_super, f100, c250, c330), BAS (Cambridge, UK; mk13, mk14, mk18, mk15, mk19, mk3, mk4, mk7) or Biotrack (Wareham, UK; mk4093, mk4083, mk3006, mk3005) geolocator-immersion loggers (hereafter 'immersion logger') fitted on the tarsus (electronic supplementary material, figure S1). Immersion loggers were programmed to test for salt-water immersion events every 3 s and record the total number of events every 10 min. Immersion could, therefore, vary between 0 (no immersion in 10 min) and 200 (complete immersion for 10 min). Loggers were typically retrieved in the year following deployment (electronic supplementary material, table S1). Across the study colonies, a mean of 66% of loggers were retrieved (range: 23–91%), of which a mean of 88% (54–100%)

provided data. Immersion logger masses varied between 1.8 and 3.3 g, representing between 0.45 and 0.83% of mean kittiwake body mass (approx. 400 g).

To determine the accuracy of colony visits identified from saltwater immersion data, in June 2022, an additional 15 kittiwakes breeding in colonies at the settlement of Pyramiden (78.65° 39′ N, 16.33° E) and Ossian Sarsfjellet (78.92° N, 12.44° E), in Spitsbergen, Svalbard were sampled for GPS tracking. Trips collected from these colonies were integrated into the larger dataset from Isfjorden, the region to which these colonies belong. Birds were caught during incubation using a noose pole and equipped simultaneously with a GPS logger (i-gotU GT-120) and an immersion logger (Biotrack/Lotek mk4083). GPS devices were programmed to take fixes every 10 min and remained on the birds for a mean of 5.3 days. GPS loggers were attached to the birds' dorsal feathers using thin strips of marine tesa® tape; immersion loggers were mounted on the birds' metal rings using two small cable ties. Total equipment mass per individual was 14.8–15.4 g, representing 3.7–3.9 % of a bird's mass (mean ± s.d. = 398 ± 39.7 g). Although deployment of GPS loggers in kittiwakes is known to affect activity budgets [37], the purpose of this analysis was to validate the use of immersion loggers for identifying colony visits, so any potential impact is unlikely to affect our results [37,38]. All GPS-tagged birds returned to the nest within a few minutes following release, and all GPS loggers were retrieved successfully.

(a) Statistical analyses

All statistical analyses and data processing were carried out in R v. 4.3.1 [39]. We interrogated fitted models by conducting diagnostic checks, including visual examination of residuals for normality, patterns or trends and assessing overdispersion using dispersion ratio checks. Results are presented as means ± s.d. or (95% confidence intervals) as appropriate, unless otherwise specified. Data were filtered to the breeding period by subsetting observations occurring within two weeks before the average minimum lay date and two weeks after the mean estimated fledge date (assuming an incubation period of 27 days and a fledging time of 41 days post-hatching; [31]). Breeding dates were obtained from the literature or estimated using expert knowledge (electronic supplementary material, table S2). Where breeding dates were unknown, the dates for the closest colony were used.

Because diel rhythmicity can vary in both detectability and expression, we used complementary analyses to quantify rhythm structure, strength and the temporal distribution of activity. We focused on two key metrics: raw immersion, which captures the temporal structure of water contact and non-contact states through time, and activity versus inactivity during trips to sea, which summarizes how behaviour is distributed across the diel cycle when birds are freed from colony attendance constraints.

(i) Estimation of individual diel rhythms

To examine variation in rhythmicity with latitude, we first extracted rhythm duration (period) of immersion patterns at the individual level. For each bird, we calculated total immersion per hour (i.e. the amount of time spent in water). Electronic supplementary material, table S3 provides a breakdown of the average number of continuous days of data per individual per colony. We used the R package `lomb` [40] to estimate individual periods by applying the Lomb–Scargle periodogram method, which is effective for detecting weak periodic components in unevenly sampled time series, such as those resulting from variable bird tracking durations. p-values were calculated from the exponential distribution and were used to assess the significance of the detected periods.

(ii) Latitudinal patterns in rhythmicity

Having estimated period lengths for individuals, we then tested whether period length or strength varied with colony latitude. To examine variation in period length, we first used a generalized linear mixed effects model (GLMM) with a binomial distribution to test whether the probability with which individuals exhibit significant periods depended on colony latitude. Second, we modelled absolute deviation from canonical diel periods (24 h and its harmonics, 12 and 48 h) using a GLMM with a gamma distribution, which is suitable for positively skewed continuous data. If period lengths are non-significant, we cannot reject the null hypothesis that these individuals are arrhythmic. Such individuals were, therefore, excluded from this analysis (n = 140); complete results including all individuals are provided in the electronic supplementary materials. We used a gamma distribution because absolute deviations from a 24 h period are continuous, positive and often skewed. Both models included a random intercept for individual identity to account for repeated measures.

To assess changes in the strength of rhythmicity with latitude, we fitted autocorrelation functions to each individual's hourly immersion time series. Following established methods [41,42], we quantified the strength of rhythmicity as 'peak strength', which is the difference in correlation value between the first peak and the following trough in the autocorrelation function. In simpler terms, peak strength reflects the prominence of periodic fluctuations, with higher values indicating stronger rhythmicity. We tested for an effect of colony latitude on peak strength by fitting a linear mixed effects model using the `lme4` package in R [43], including a random intercept for individual identity.

(iii) Activity patterns across the diel cycle

To investigate whether diel patterns in immersion could reflect synchronization with the Earth's photic cycle cues, we examined how hourly immersion levels varied with sun elevation angle and whether this relationship changed with colony latitude. To this end, we fitted a generalized additive model incorporating a tensor product smooth of sun elevation angle and colony

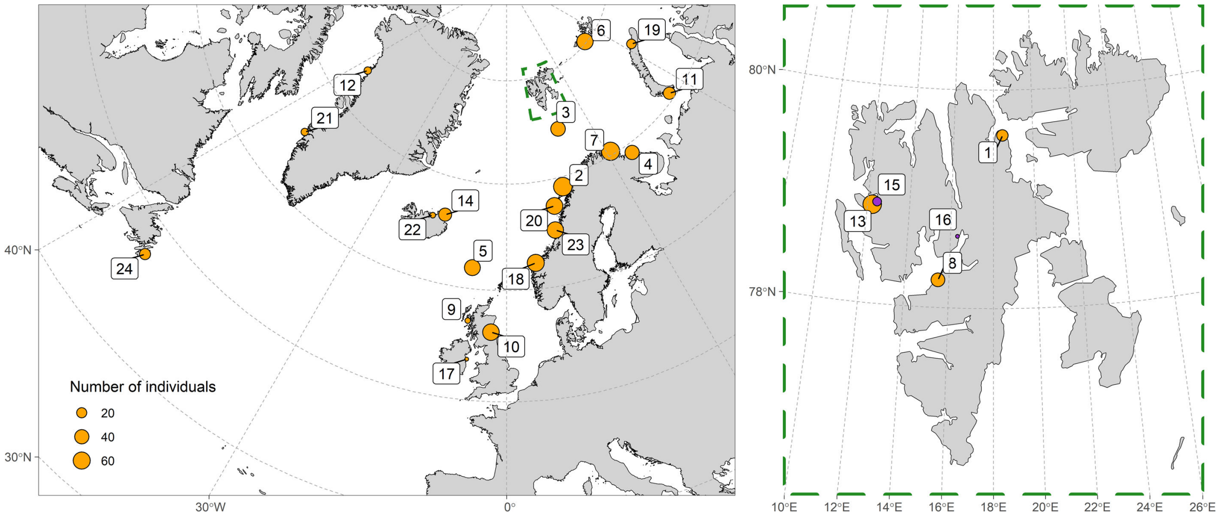

Figure 1. Locations of black-legged kittiwake colonies used in the analysis, indicated by orange points (size is relative to the number of individuals tracked at the colony). Square labels are referenced to electronic supplementary material, table S1. The right panel shows a detailed map of Svalbard, highlighting colony locations that are not visible on the main map. Colonies at which GPS tracking was carried out are highlighted in purple. Map and locations are displayed in a stereographic polar projection centred on the North Pole.

latitude to test for a nonlinear effect of hourly sun elevation angle on individual hourly immersion levels. Fitting the model to the full dataset was computationally infeasible owing to memory constraints arising from the large number of observations and the complexity of the tensor product smooth, which caused model fitting to fail. To reduce computational load while retaining biologically meaningful structure in the data, we randomly subsampled continuous 72 h intervals for each individual, ensuring that the temporal dynamics of behaviour was preserved within a manageable dataset. To ensure that our results were not overly dependent on any single subset of data, we implemented a resampling approach, repeating the subsampling 100 times and refitting the model each time. From each model, we extracted the estimated degrees of freedom (EDF) of the tensor smooth and the *p*-value for sun elevation angle and compared the distribution of these across the resampled data. Models were fitted with the `mgcv` package in R [44].

To complement the analyses on raw immersion data, and specifically to link patterns in diel organization to ecologically meaningful behaviours, we classified time spent at sea into broad 'active' and 'inactive' states, to examine whether the timing and distribution of activity vary predictably with latitude.

We first separated probable trips to sea from colony attendance using the raw immersion data. Briefly, since birds do not encounter salt water at the colony, extended bouts of high or fluctuating immersion levels, lasting significantly longer (>50 min) than brief departures to water close to nests, probably indicate time spent at sea; this was validated using trips identified using GPS data, from which we obtained a mean 87.0 ± 12.7% accuracy (for details see electronic supplementary materials). Next, during trips to sea, we classified behaviour into active (flight or foraging) or inactive (resting on the water) states. Intervals of 10 min with ≥90% wet time and surrounded by intervals that also had ≥90% wet time were considered inactive, while all other intervals were considered active. This approach was inspired by previous methods used to classify behaviour from immersion data in kittiwakes [45,46], which have also been validated using GPS [47], electronic supplementary material, appendix S1).

We explored changes in activity with time of day to assess whether activity levels distribute throughout the day at high latitudes. To this end, we fitted a generalized additive mixed model (GAMM) using a tensor product smooth to capture the joint effect of hour of day and colony latitude on activity (binomial response, active/inactive). The model included a random intercept for individual identity to account for repeated measures. To test whether the timing of activity varied with latitude, we compared two GAMM structures: (i) an additive model with separate smooth terms for time of day (hour, modelled cyclically) and colony latitude; (ii) an interaction model employing a tensor product smooth between time of day and latitude, allowing the effect of time to vary flexibly with latitude. We fitted models using the `mgcv` package with fast restricted maximum likelihood (fREML) estimation for computational efficiency. We compared models via Akaike Information Criterion (AIC) and likelihood ratio tests.

3. Results

(a) Estimation of individual diel rhythms

The period length ranged from 4.05 to 48.0 h, with an overall median of 24.0 h and a mean of 27.4 h (figure 2; electronic supplementary material, table S3; n = 971). The majority of birds across colonies had significant periods (82%), suggesting that most individuals exhibited rhythmic activity. Visualization of mean daily changes in immersion (figure 3), actograms for immersion (electronic supplementary material, figure S5) and individual autocorrelation functions (electronic supplementary material, figure S6) indicated a tendency for individuals breeding in lower-latitude colonies to have more regular periods of approximately 24 h.

(b) Latitudinal patterns in rhythmicity

The proportion of birds exhibiting rhythmicity did not vary with colony latitude ($\beta = 0.046 \pm 0.0066$, $z = 0.70$, $p = 0.48$; $n = 971$ individuals; electronic supplementary material, figure S7). Correspondingly, higher-latitude colonies showed greater deviations from a 12-, 24- or 48 h period, with an approximate 12% increase in the deviation for each degree increase in latitude ($\beta = 0.12 \pm 0.0085$, $t = 13.92$, $p \leq 0.0001$; $n = 831$; figure 4A, electronic supplementary material, figure S8).

Median peak strength—our measure of the strength of rhythmicity—was 0.74. Peak strength declined significantly, though modestly, with increasing colony latitude: the coefficient estimate was -0.0036 ± 0.000037, meaning that for each degree increase in latitude, peak strength decreased by approximately 0.5% ($t = -9.79$, $p < 0.0001$; $n = 971$; figure 4B). This indicates that the strength of rhythmicity in immersion levels declined with increasing latitude.

(c) Activity patterns across the diel cycle

Sun elevation angle and colony latitude jointly explained variation in immersion levels, with a highly significant, nonlinear interaction (EDF = 23.28, $F = 309.00$, $p < 0.0001$; $n = 971$). When the sun elevation angle was <0° (in other words, the sun had dipped below the horizon), immersion levels increased substantially, especially at lower latitudes (electronic supplementary material, figure S9). The model explained 27.3% of the deviance in immersion. There was no evidence to suggest that the selection of our sample influenced results. Mean EDF across models fitted to randomized datasets was 22.79 ± 0.66 (s.d.; electronic supplementary material, figure S10). The p-value for the effect of sun elevation angle and colony latitude was <0.0001 for all models.

We found that the model including the interaction of colony latitude and hour of day provided a significantly better fit than the additive model (likelihood ratio test: ΔDeviance = 790 015 on 12 d.f., $p < 0.0001$; ΔAIC = 789 991), indicating that the daily timing of activity varies across latitudes. The tensor product smooth for colony latitude and hour of day was highly significant (EDF = 17.0, $\chi^2 = 914\,378$, $p < 0.0001$; $n = 971$), suggesting that diel activity varies with latitude, consistent with latitudinal variation in rhythmicity (figure 5). Specifically, lower-latitude colonies showed distinct peaks in activity at dawn and dusk, while higher-latitude colonies showed flatter activity responses. The model explained approximately 2.2% of the deviance (adjusted $R^2 = 0.030$), typical for high-variability biological data with random effects.

4. Discussion

Animals breeding in polar regions show diverse behavioural responses to 24 h daylight, ranging from strict 24 h rhythmicity [48–50], to consistent rhythms deviating from 24 h [22,51] and an apparent absence of rhythmicity in the circadian range [52,53]. In our study, the degree of rhythmicity in activity varied across colonies: at low latitudes, kittiwakes exhibited consistent 24 h rhythmicity, while kittiwakes at high-latitude colonies displayed much more variable periods that consistently had a median value of over 24 h, suggestive of 'free-running-like' rhythms—that is, self-sustained rhythms that are not apparently synchronized with external cues. While both among- and within-species variation in diel rhythms have been documented in wild vertebrates [54–57], our study demonstrates that diel rhythmicity can vary systematically across multiple populations within a single species, probably reflecting adaptation to local light environments.

The finding that kittiwakes express periods that vary considerably among populations aligns with evidence from other high-latitude animals showing substantial within- and between-population variation in rhythmicity [18,22,54–56]. Collectively, these findings suggest that the responses of animals to the attenuation of diel cycles are likely to be species- or even population-specific, rather than a universal phenomenon. Although we could not account for variation in breeding stage, which is known to influence foraging effort and rhythmicity in other species [18,22,27], it is notable that activity patterns at high-Arctic colonies were consistently flat across the 24 h day despite including a mix of incubating and chick-rearing individuals. It is important to note, however, that rhythmicity did not disappear altogether or revert to ultradian rhythms mirroring digestive cycles, which might be expected if the behaviour were solely about optimizing the exploitation of available light. This suggests that other factors, such as energy balance, internal biological rhythms or prey availability, may influence kittiwake behaviour, indicating a more complex relationship between the species and environmental cues than a simple light-driven rhythm.

Activity levels of all birds correlated strongly with the sun's elevation angle, with high immersion levels (associated with resting on the water) peaking when the sun dipped below the horizon, suggesting that 24 h activity rhythms in this species are primarily driven by the light–dark cycle. At lower latitudes, birds exhibited distinct diel rhythms with two clear peaks of activity corresponding to dawn and dusk, consistent with a reliance on light cues for foraging and rest. By contrast, kittiwakes at high-latitude colonies exposed to continuous daylight showed flattened activity patterns across the 24 h cycle, suggesting a loss or dampening of diel rhythmicity under these extreme photic conditions. This departure from strict diel rhythms may enable birds to forage opportunistically throughout the day, which could be advantageous given that their key prey species, including *Thysanoessa* krill and Arctic cod, lack photoperiodic behaviour and may therefore be consistently available. However, it is important to note that local factors, such as proximity to productive foraging areas [58] and colony size [59], could also contribute to observed differences in activity timing by influencing factors such as foraging trip duration or competition for resources.

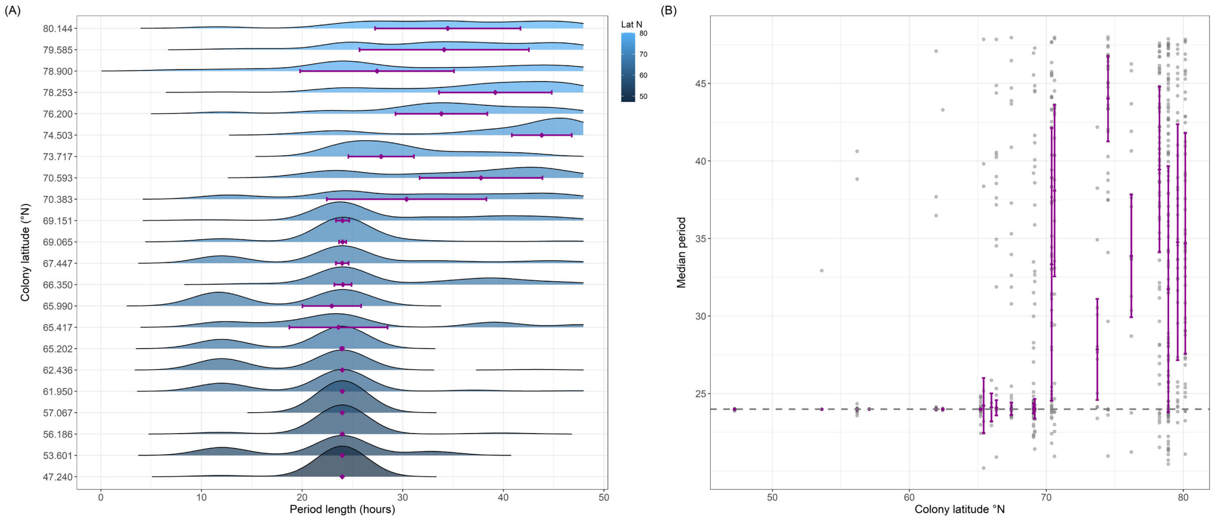

Figure 2. (A) Ridge plot showing distribution of individual period lengths, estimated from raw immersion data using Lomb–Scargle periodograms, in descending order by colony latitude. Ridge colour indicates colony latitude, with lighter blue indicating more northerly colonies. All period lengths, regardless of significance, are included in the panel ($n = 971$). (B) Median period (hours) plotted against colony latitude. The grey dashed line starts at $y = 24$ h. In this plot, only individuals with significant periods are included ($n = 831$). In both plots, purple points and horizontal (panel A) and vertical (panel B) lines indicate the overall median and deviation for each colony.

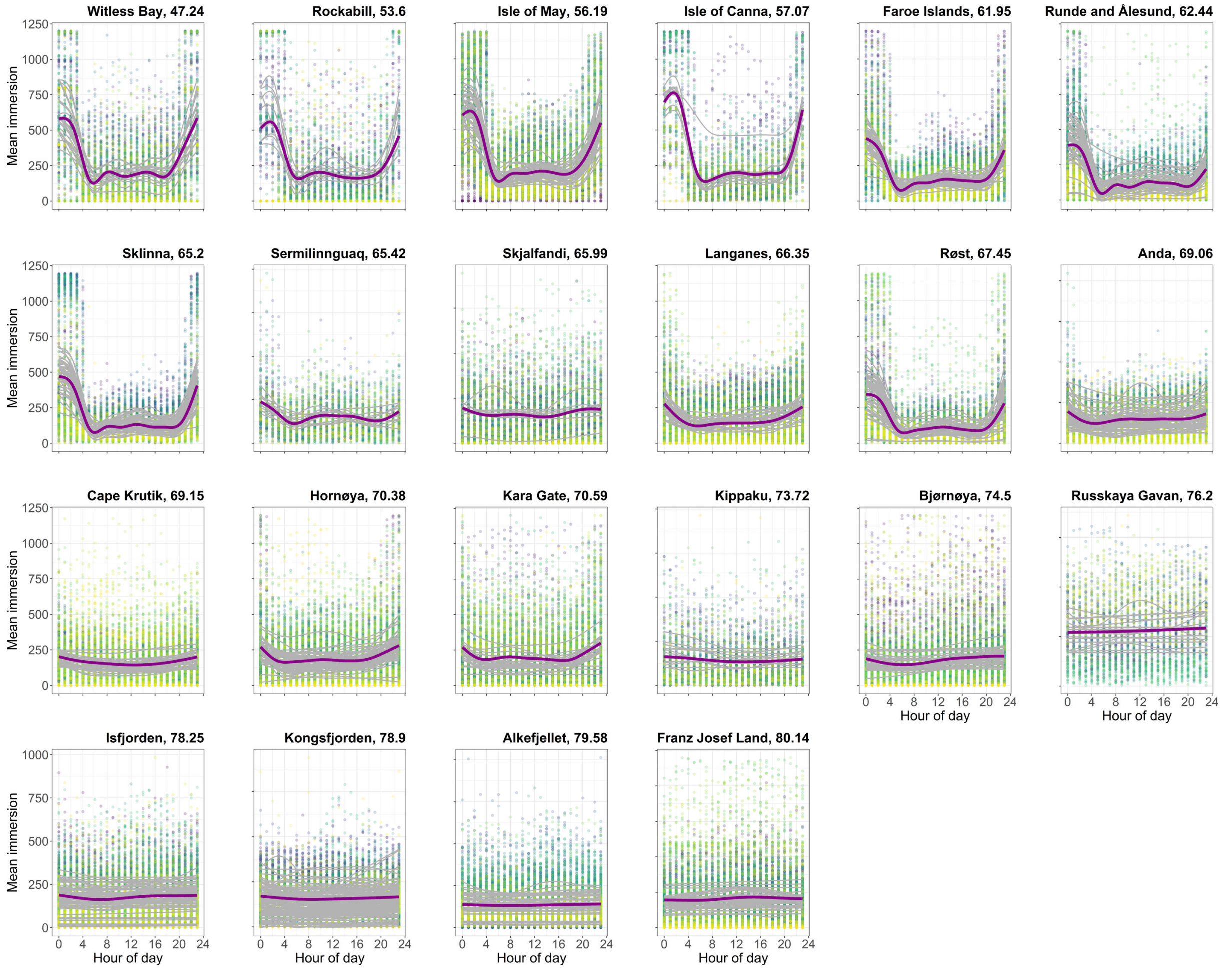

Figure 3. Mean hourly immersion values across the entire colony, with one plot per colony, ordered by increasing colony latitude. Each data point represents the average immersion value for a single hour of the day, averaged across all tagged individuals for that colony. Colours distinguish different days. Loess-smoothed curves show temporal trends: grey lines represent individual birds, while the purple lines indicate the colony-level averages.

While we were unable to assess chick growth or meal delivery rates directly, temporal flexibility in activity patterns may be particularly important during chick-rearing. Seabird provisioning takes place in variable environments where food supplies vary—spatially and temporally—in both availability and quality, meaning that chicks may experience prolonged bouts of fasting between feedings. For kittiwakes, the nestling growth rate is best predicted by the a combination of meal delivery rate and size, rather than energetic content alone, probably owing to digestive efficiency or energy storage capacity limits [60,61]. Consequently, the ability to forage throughout the 24 h day could allow parents to maintain consistent meal delivery rates,

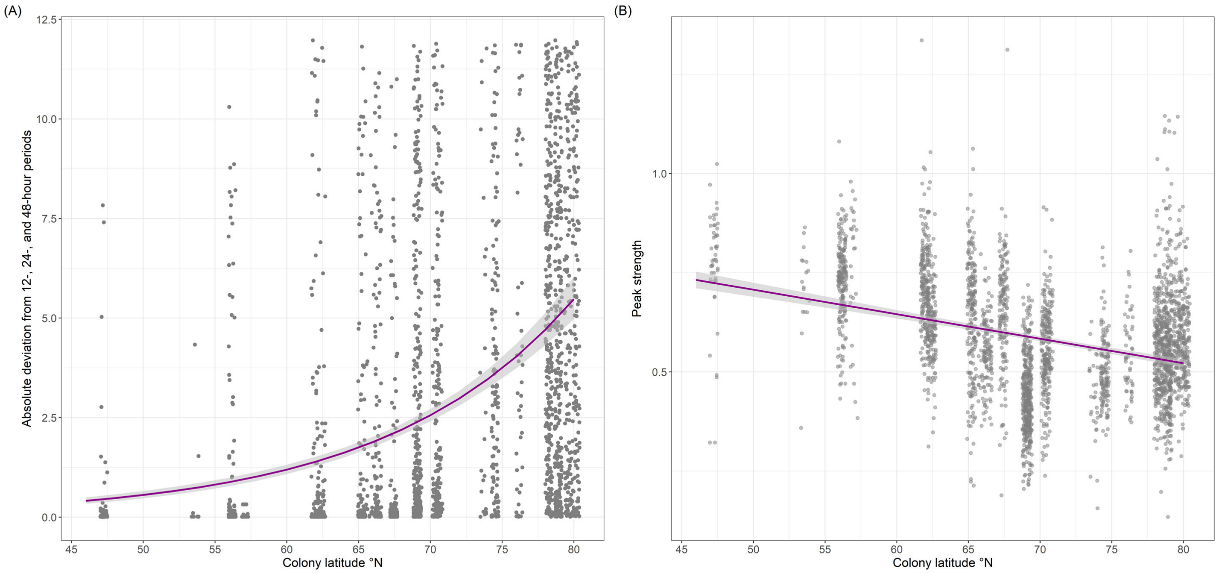

Figure 4. (A) Absolute deviation from 12-, 24- and 48 h periods as a function of colony latitude. The purple line and shaded grey interval indicate regression and 95% confidence intervals from a generalized linear model with a gamma error distribution. Points indicate period lengths for individual birds at each colony and are subset to individuals with significant periods ($n = 831$). Each point indicates an individual bird's period; points are 'jittered' in x-axis for readability. (B) Peak strength, reflecting the prominence of periodic fluctuations, as a function of colony latitude, in degrees. Higher peak strength values indicate stronger rhythmicity. The purple line indicates the regression of colony latitude on peak strength; shaded grey areas indicate 95% confidence interval of the mean. Each point represents the mean peak strength value for an individual.

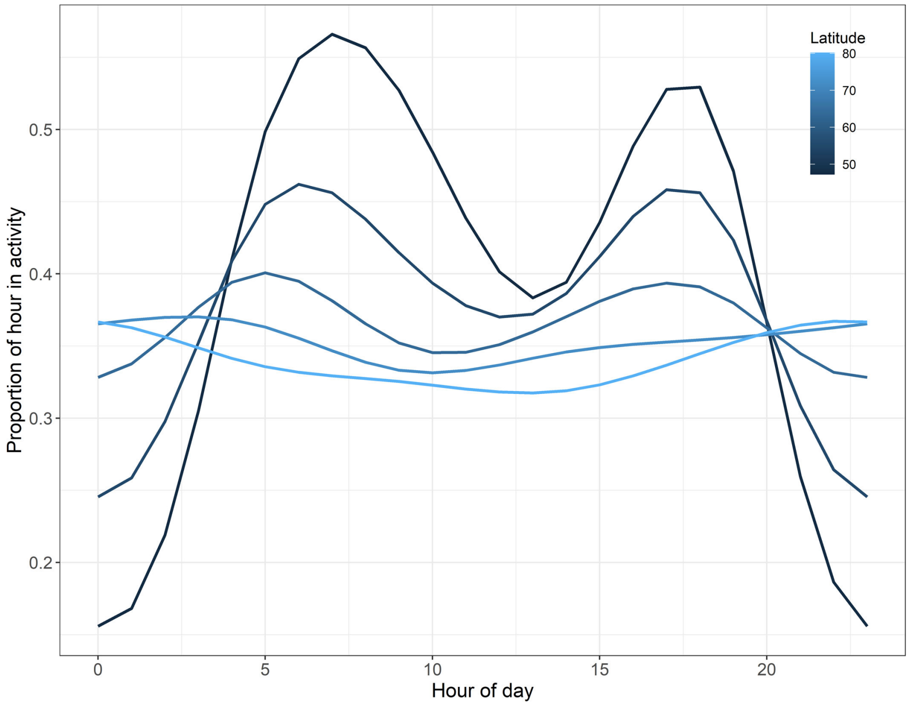

Figure 5. Predicted diel activity patterns by latitude, from a generalized additive model examining the proportion of each hour spent active across the 24 h day as a function of both latitude and time of day. Predictions are shown for five evenly spaced values of colony latitude. Lines represent model predictions; colours indicate latitude, with lighter hues corresponding to more northerly colonies.

reducing the amount of time that chicks must fast between meals. Conversely, at lower latitudes, as kittiwakes are presumed to be visual predators [31], light availability constrains nighttime foraging, meaning that parents cannot provision continuously even if prey is available. Future research using data where exact breeding timings are available should explicitly investigate whether provisioning frequency increases in high-latitude colonies and whether this has positive impacts on reproductive success.

Our results demonstrate that black-legged kittiwakes show strong population-level variation in diel activity patterns across a wide latitudinal gradient, with marked differences between colonies exposed to continuous daylight and those experiencing a light–dark cycle. These clear, broad-scaled patterns support the idea that light availability is a key driver of activity rhythms in this species. While we acknowledge that various factors, including breeding status, colony characteristics and local environmental conditions, are also likely to contribute to our observed activity patterns, our datasets did not allow these effects to be fully disentangled. Future work building on these findings should explicitly integrate such local factors to better understand how they interact with large-scale environmental cues to shape temporal behavioural flexibility. Nonetheless, our study highlights the importance of considering temporal flexibility as an important, and sometimes under-recognized, axis of behaviour variation that merits further attention.

Ethics. Fieldwork with kittiwakes in multiple locations was conducted with appropriate permits and permissions. In Canada, approval was granted by Environment and Climate Change Canada's Eastern Wildlife Animal Care Committee (projects 19GR01, 20GR01, 21GR01, 22GR01 and 23GR01). In Greenland, fieldwork was approved by the Agency of Fisheries, Hunting and Agriculture. Icelandic ringing licenses were obtained from the Icelandic Institute of Natural History, with ethics approval granted by the Icelandic Food and Veterinary Authority (2019-01-10, 2204585). In Norway, data collection was authorized by the local County Governors and the Governor of Svalbard (Sysselmesteren på Svalbard; RiS ID: 11820, 6920 and 361), with ethics approval from the Norwegian Food Safety Authority (Mattilsynet; FOTS ID 29584) and ringing licenses issued by the Norwegian Environment Agency (Miljødirektoratet) and Stavanger Museum. On the Isle of May, UK, annual National Nature Reserve permits were provided by NatureScot (MON/RP22/4 for 2022 and its predecessors) and permits to deploy data loggers were provided by BTO's Special Methods Technical Panel (SMTP; permit 2046).

Data accessibility. Summarized data supporting the results as well as associated scripts to conduct the analyses can be accessed on Zenodo [62].

Supplementary material is available online [63].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

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