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Research article

Flexibility in the diel migratory schedule of an Arctic songbird despite robust 24-h activity rhythms across the annual cycle

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Many birds schedule their activity to a specific phase of the diel (24-h) light–dark cycle. Two notable exceptions are the nocturnal migration of many otherwise diurnal songbirds and the diverse activity patterns of birds during the continuous light above the Polar Circles during summer. Assumptions about the phase relationship between migratory activity and the diel cycle can be incorrect, and the diel activity of Arctic migratory birds during the year is largely unknown. We used the snow bunting *Plectrophenax nivalis* to investigate whether breeding songbirds above the northern Polar (Arctic) Circle have 24-h activity rhythms with distinct active and inactive phases across the annual cycle, and whether their migration aligns with a specific phase of their activity rhythm. We found that male snow buntings maintain a robust 24-h activity rhythm with distinct active and inactive phases across most of the annual cycle, including during polar summer, but the robust 24-h periodicity attenuated during vernal migration. Birds scheduled long and short flights across their diel activity rhythm. However, shorter flights most often began during the active phase, and the longest flights most often began during the transition between the active and inactive phase of the diel activity rhythm. This indicates that snow buntings can flexibly schedule their flights across their prominent diel activity rhythm, although their longest flights during migration typically overlapped with their normal inactive phase, probably corresponding to nighttime. Several open questions, however, remain about the generality of our results for other songbirds, such as: what is the phase relationship between the

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diel activity rhythm and flight to the diel light–dark cycle, and how do historical accounts of diel migration phase align with empirical activity data for other species?

Keywords: annual activity, Arctic bird, chronobiology of bird migration, daily activity rhythm, daily migration timing, flexible migration strategy, sideral day, snow bunting, songbird migration

Introduction

Diel activity patterns (Glossary) in birds generally couple tightly with the *diel* geophysical light–dark cycle (Helm et al. 2017, Kumar 2017, Gilbert et al. 2022, Vallejo-Vargas et al. 2022, c.f. Bloch et al. 2013). Indeed, many birds schedule their activity consistently during one specific *phase* of this *diel cycle*. For example, *diurnal* animals primarily have a *diel activity rhythm* with the active phase during daylight and an inactive phase during nightdark. Two notable exceptions to this general pattern are the migratory flights of many birds, including *nocturnal* migration of otherwise diurnal birds (Alerstam 1990, Newton 2008), and the diverse activity patterns of birds during the continuous light of polar summer, which range from arrhythmicity and non-24-h rhythms (Reierth and Stokkan 1998, Lesku et al. 2012, Steiger et al. 2013) to 24-h rhythms that align, sometimes oppositely, to the diel cycle (Ashley et al. 2013, Huffeldt and Merkel 2016). However, the diel scheduling of migration in polar birds is largely unknown, and the general assumption that migratory flights of many species are either in phase or antiphase with a general diel activity pattern (Newton 2008, Adamík et al. 2016) is often based on limited or historical observations, and high-resolution tracking can contradict these expectations (Briedis et al. 2020).

Some groups of birds, such as waterfowl and waders, may have a weak *diel rhythm* in migration or activity (McNeil et al. 1992, Helm et al. 2012), including above the northern Polar (Arctic) Circle (Steiger et al. 2013, Bulla et al. 2016). However, this is not expected to be common in songbirds (Newton 2008), as 79% of 70 examined songbird species that migrate from Europe to sub-Saharan Africa are thought to align their migratory flights to only one phase of the diel light–dark cycle (Adamík et al. 2016). Additionally, songbirds breeding near or above the Arctic Circle appear to maintain 24-h *periodicity* that aligns with the diel cycle of solar altitude. Lapland longspurs *Calcarius lapponicus*, a migratory songbird that breeds under polar day, maintain strict *circadian rhythms* entrained to the 24-h light cycle (Ashley et al. 2013, 2014), while other migratory songbirds, willow warblers *Phylloscopus trochilus* and northern wheatears *Oenanthe oenanthe*, reduce activity during the lowest light intensities of the diel cycle near and above the Arctic Circle (Asbirk and Franzmann 1979, Silverin et al. 2009). Additionally, 'nocturnal' migration during the lowest diel light intensities does not seem to cease during the continuous light of polar summer (Nilsson et al. 2015).

One hypothesis proposed for songbirds that maintain a strict diel rhythm, most likely driven by a circadian rhythm (Gwinner 1996, Ashley et al. 2014), during polar day is that the rhythm is necessary for keeping an internal calendar for scheduling annual phenological transitions across the year (Gwinner 1986; see also Appenroth et al. [2021] for discussion on maintaining circadian rhythms for photoperiodic scheduling in a non-songbird). The maintenance of an internal calendar based on a diel rhythm may trump the temporary advantage of continuous activity that can facilitate energy acquisition (van Oort et al. 2007, Williams et al. 2015) or

Glossary. Definitions of key chronobiology terms. Most definitions adapted from Gilbert et al. (2022), Hazlerigg et al. (2023), and www.circadian.org/dictionary.html (last accessed 2025-02-06).

Circadian rhythm	An endogenous rhythm originating from within an organism that has a period of approximately 24-h. To be considered a circadian rhythm several criteria must be met, including endogenous generation and entrainment to external cues (see Gilbert et al. 2022, Hazlerigg et al. 2023).
Diel	Having the duration, or period, of a 24-h day. Diel should not be used as a synonym of diurnal.
Diel cycle	Synonymous with 24-h geophysical day, but less ambiguous than 'day' because 'day' may be confused with daytime or the light phase of the day.
Diel rhythm	A repeated sequence of events aligning with the 24-h rotation of the Earth. Diel rhythms have a period of 24 hours. Circadian rhythms are diel rhythms, but not all diel rhythms are circadian rhythms. 'Daily rhythm' is synonymous with diel rhythm.
Diel activity pattern	The arrangement of behavior and movement across a diel cycle.
Diel activity rhythm	A diel activity pattern that is a diel rhythm with a period of 24-h. Typically has one active phase with much movement and one inactive phase with less to no movement.
Diurnal	Occurring or active during daylight or the light phase of the diel cycle. Diurnal should not be used as a synonym of 'diel' or 'daily' because diurnal may be confused with occurring or active during daylight.
Nocturnal	Occurring or active during nightdark or the dark phase of the diel cycle.
Period	The time elapsed for one complete oscillation or cycle (e.g. the duration between two consecutive peaks).
Periodicity	The state of having a period or periodic structure.
Phase	A distinct stage of a process (e.g. the active phase of a diel activity rhythm; the dark phase of a light–dark cycle; or the breeding phase of an annual rhythm).
Sidereal day	The rotation of the earth on its axis relative to distant stars with a period of 23.93 h.
Solar day	The diel light–dark cycle caused by one rotation of the earth on its axis relative to the sun with a period of 24 h.

mating opportunities (Lesku et al. 2012) across the diel cycle when the sun does not set. However, no one, to our knowledge, has tested the hypotheses that Arctic migratory birds maintain 24-h periodicity in their activity across the annual cycle, or that songbirds breeding under polar day have more flexible expression of migration scheduling relative to their diel activity rhythm. Another missing aspect in the literature is that many descriptions of nocturnal and diurnal migration in wild, free-living birds describe the phase relationship between the migratory activity and the light–dark cycle but do not assess whether birds maintain a diel activity rhythm when migrating, or whether the migratory activity aligns with a specific phase of a presumptive diel activity rhythm (c.f. Bäckman et al. 2017a, Briedis et al. 2020, Macías-Torres et al. 2022).

A major limitation in addressing these gaps has been technological deficiencies (c.f. Bäckman et al. 2017b). With the advent of small multisensor data loggers, activity data from small birds can be collected across the annual cycle at high temporal resolution (Bäckman et al. 2017a, Liechti et al. 2018). We used this advancement in technology with a small migratory songbird, the snow bunting *Plectrophenax nivalis*, to test the two hypotheses stated above. Snow buntings appear to align activity to the diel cycle above the Arctic Circle, with the lowest frequency of nest visits during the lowest light intensities (Krüll 1976, Meltofte 1983), and historical observations suggest that snow buntings may migrate during both day and night (Parmelee 1968, Montgomerie and Lyon 2020), while others classify the snow bunting as a nocturnal migrant (Horton et al. 2019). Generally, a presumed diurnal or nocturnal migrant only extends migratory flights into the opposite diel phase when crossing ecological barriers (Adamík et al. 2016, Ouwehand and Both 2016, Liechti et al. 2018, Sjöberg et al. 2021, Norevik et al. 2023), yet accepted assumptions about the phase relationship of migration to the diel cycle in songbirds may be misleading (Briedis et al. 2020). Therefore, individual tracking is required to understand the scheduling of the snow bunting's migration, and we used the snow bunting to address two overarching questions: 1) what is the diel activity pattern of the snow bunting across the annual cycle, and 2) does this Arctic-breeding songbird migrate according to a specific phase of a diel activity rhythm? We used custom multisensory data loggers to identify the diel activity pattern of individual snow buntings across the full annual cycle; identify when during an individual's diel activity pattern they initiated migratory flights; and quantify how long snow buntings flew during their active and inactive phases of their diel activity pattern.

Material and methods

Study species and field site

Snow buntings can breed well above the Arctic Circle across the Northern Hemisphere (Montgomerie and Lyon 2020). High latitude populations are migratory and may complete their molt quicker than their more southern conspecifics, presumably to finish molt before migration (Green and Summers 1975). During winter snow buntings can either remain in an overwintering site or move nomadically among sites (Snell et al. 2018, Mckinnon et al. 2019, Montgomerie and Lyon 2020).

Our study birds were part of a nestbox population in Adventdalen near Longyearbyen, Svalbard, Norway (78°12'N, 15°48'W) that are included in a long-term monitoring scheme (Fossøy et al. 2015). The birds depart the Svalbard archipelago in mid-September, flying eastwards towards Novaya Zemlya or the eastern Kola Peninsula before moving southwards and arriving at their overwintering grounds on the western steppe of Siberia between mid-October and early-November (Snell et al. 2018). In spring, they begin moving northward towards Svalbard via the Kanin Peninsula, northern Fennoscandia, or Novaya Zemlya at the beginning of April (Snell et al. 2018). During transit to and from the overwintering grounds, Svalbard snow buntings generally take relatively short flights, except when crossing the Barents Sea, a distance of approximately 850 to 1100 km (Snell et al. 2018).

Data logger deployment

During the summer of 2017 and 2018, a total of 16 male adult snow buntings breeding on Svalbard were equipped with multisensor data loggers (13 males in 2017 and five males in 2018; two males had their loggers replaced in 2018, resulting in 18 loggers attached in total; see below). Loggers were attached using a leg-loop harness (the mass of the data logger plus attachment material was < 1.2 g; between 3.0 to 3.7% of the body mass of the birds). Eight data loggers from seven birds were retrieved in the summers after deployment (one additional bird was also recaptured, but its logger was lost). One individual was equipped with two different loggers in consecutive years, resulting in data from two full annual cycles. Another individual was recaptured after two years, and its data logger recorded two full annual cycles. One individual's data recording stopped in May during its first annual cycle. This study thus includes data from seven individuals and approximately 9.8 annual cycles (n = 7 males: 5 recaptured after one year, 1 recaptured twice and carrying two different loggers, 1 recaptured after two years; Huffeldt et al. 2025).

The custom multisensor data loggers included an accelerometer, a temperature-compensated barometric-pressure sensor (recording both barometric pressure and temperature; however, this sensor malfunctioned in most loggers deployed in 2017), a light-level sensor, a real-time clock, and memory (Bäckman et al. 2017a, Sjöberg et al. 2018). To optimize memory, light was recorded for five 5-day blocks throughout the year, programmed to make it possible to find the position of the birds during potential stationary bouts. The light data, however, only allowed localizing the birds in five out of the eight data loggers included in the analysis, and only from November to January (Supporting information; localization relied on: Ekstrom 2004, Lisovski et al. 2012, Lisovski and Hahn 2012). Therefore, in this study, we focused on accelerometer data to estimate the detailed activity of the birds throughout the full annual cycle.

The accelerometer measured acceleration on a single axis (approximately vertical during flight) and was customized to detect activity (Bäckman et al. 2017a). One sample was recorded every 5 min, and the data was aggregated per hour (h) in UTC (i.e. 'sampling hour'). Each 5-min sample consisted of five subsamples (100 ms duration at 100 Hz) with 5 s spacing. If all five subsamples detected activity (acceleration varied more than ¼ g), the 5-min sample scored '5'. If no subsamples detected activity, the sample scored '0'. Intermediate cases scored '1' to '4' (for a detailed description of the function and measurement scheme, see Bäckman et al. [2017a]).

Since we did not have access to the full year of light-level data, we used the activity rhythm to relate the timing of migratory movements to each individual's inactive and active phase of their diel activity rhythm. Therefore, the presentation of results and our discussion focuses on the phases of activity relative to the diel activity rhythm and not relative to the diel light–dark cycle or time of day. Because of the snow bunting's presumed diurnal activity patterns (Parmelee 1968, Krüll 1976, Meltofte 1983, Montgomerie and Lyon 2020), the assumption could be made that the active and inactive phases of the diel activity rhythm represent daytime and nighttime, respectively, outside of polar day. In this study, however, we cannot, and do not attempt to, assess whether phases of activity align with specific phases of the diel cycle, except when at the known breeding site.

Periodicity analyses

We used R ver. 4.4.1 for all data handling and analyses (www.r-project.org). We identified periodicity across the annual cycle using wavelet analysis. Wavelet analysis allows for detecting changes in periodicity within a provided window of 'periods' across a continuous time-series (Cazelles et al. 2008, Leise 2013, van Beest et al. 2020). Following van Beest et al. (2020), we used the R-package 'WaveletComp' (Roesch and Schmidbauer 2018) and the white noise method with 100 bootstrap simulations to test whether a periodic structure occurred in each individual time-series of activity data. In the wavelet analyses, we included all accelerometer data (as cumulative activity score per hour), including incomplete time-points caused by logger malfunction (missing data: [bird ID XA49] n = 1 of 6633 h; [bird ID X0A7] n = 10 of 17139 h). We used a periodicity window of ¼ to 2 periods (i.e. 6 to 48 h), with 1 period equal to 1 diel (24-h) cycle.

Because of the incomplete data points included in the wavelet analysis, we also completed a randomized Lomb–Scargle periodogram (LSP) analysis using the R-package 'lomb' (Ruf 1999) to confirm and easily summarize periodicity. LSP analysis robustly detects periods in time-series with missing data (Ruf 1999, Huffeldt and Merkel 2016). We used 1000 repeated randomizations, an oversampling factor of five, and a period window of 0 to 48 h (Huffeldt and Merkel 2016). The input data were individual time-series split by month, which provided a rough delineation to summarize periodicity across the annual cycle. We report the mean, the standard deviation (SD), median, and the 95% confidence interval (CI) of the period with the largest test statistic (PN_{max}) for each month of an annual cycle (Huffeldt and Merkel 2016).

Identifying phases of diel activity rhythms and flights

To identify the time of day (UTC) for activity onset and offset, we used the timestamps corresponding to the 2 and 95% quantiles, respectively, of the day's total activity distribution based on all activity scores recorded between 00:00 and 23:59 (Fig. 1). We chose these quantiles based on how activity phases matched actograms. Supplementary actograms depict how the estimated times of activity onset and offset align with measured activity (Supporting information). We calculated the exact times of onset and offset of daily activity by subtracting the minutes corresponding to the number of 5 min samples with an activity score > 0 from the sampling hour, assuming that all samples within a sampling hour with activity score 0 belonged to the same inactivity bout. For only one individual (bird ID X0A7) during two days in May, this method did not correctly estimate activity phases when flights also occurred. For these two days, we manually

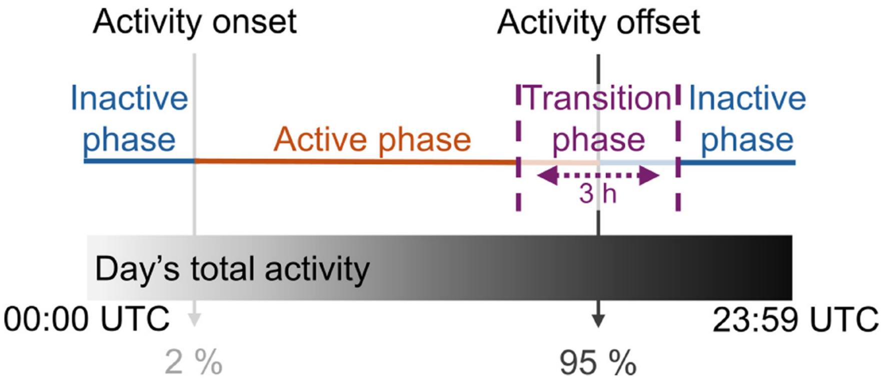

Figure 1. Depiction of the classification of activity onset and offset and activity phases used in analyses. Activity onset was defined as the 2% quantile of the day's total activity. Activity offset was defined as the 95% quantile of the day's total activity. For analyses linking flights to activity phases, we used the mean time of day (UTC) of phases for the 3.5 days preceding a flight.

estimated activity offset using values for preceding days identified using the individual's actogram before analyzing flights.

We defined three phase categories of the diel activity rhythm ('active', 'transition', and 'inactive') using the times of day for the onset and offset of activity to be used in subsequent analyses of flights. The active phase was defined as the mean time of activity onset for the 3.5 days preceding a flight up to the start of the transition phase (Fig. 1). The transition phase was the 3-h phase of the diel activity rhythm centered on the mean time of activity offset for the 3.5 days preceding a flight (Fig. 1). The transition phase thus corresponds to 1.5 h before to 1.5 h after the bird on average stopped being active during the 3.5 days prior to a flight, and represents the phase in which migratory flights may be expected to be initiated for diurnal songbirds that employ a nocturnal migration strategy (Alerstam 1990, Newton 2008). The inactive phase was defined as from the end of the transition phase to the mean time of activity onset for the 3.5 days preceding a flight (Fig. 1).

We classified that a flight occurred during an hour of the day (UTC) if the following four criteria were met: 1) an hour had a cumulative activity score > 30; 2) at least one 5-min sample with activity score = 5; 3) no 5-min sample with activity score = 0; and 4) either the previous or following hour had at least one 5-min sample with activity score > 0. We additionally classified a single hour of non-flight as flight that was between two hours designated as flight; this only occurred in 23 instances out of 305 designated flights and mainly occurred (18 instances) because criteria 1 and 2 were not fulfilled for the single hour. Based on the assumption that activity scores 2 to 5 in the hour before and in the hour after categorized flight activity were part of the same migratory flight, we calculated the assumed start time of the flight by subtracting the minutes corresponding to the number of 5-min samples with activity score from 2 to 5 of the preceding sampling hour from the first hour with full flight activity. Correspondingly, we calculated end time of the flight by adding the minutes corresponding to the numbers of 5-min samples with activity score from 2 to 5 of the following sampling hour to the last hour with full flight activity. We calculated flight duration by summing the number of 5-min samples with an activity score from 2 to 5 and multiplying the sum by five. We defined 'shorter' and 'longest' flights by identifying the 90% quantile of flight duration, and we categorized the longest 10% of flight durations as 'longest' flights and all flights with durations less than this cutoff as 'shorter' flights. We chose this cutoff because the aim was to identify the diel scheduling of the longest flights associated with larger scale movements that are most likely migratory and shorter flights that may or may not be associated with migration or smaller scale nomadic movements (Fig. 2; Snell et al. 2018, Montgomerie and Lyon 2020). We excluded the months of June, July, and August from flight analyses because the birds bred at this time, and, therefore, these flights could not be related to larger scale movements or migration.

Analyses of activity phases

To quantify the duration of the inactive and active phases across the annual cycle, we calculated the difference between the start and end of the active phase and the start and end of the inactive phase using the estimated time of activity onset and offset, respectively. Because actograms for each individual indicated that inactive phases ≤ 1 hour do not occur (Supporting information), we removed all inactive phases classified (using our criteria above) as ≤ 1 hour and active phases ≥ 23 h before analysis of durations of activity phases. Keeping the data does not change the statistical significance or the pattern of the results (Supporting information). We calculated the mean duration of activity phases with SD, median, and 95% CI for each month. To understand how the duration of activity phases changed, we modeled phase duration as a function of the interaction between the circular

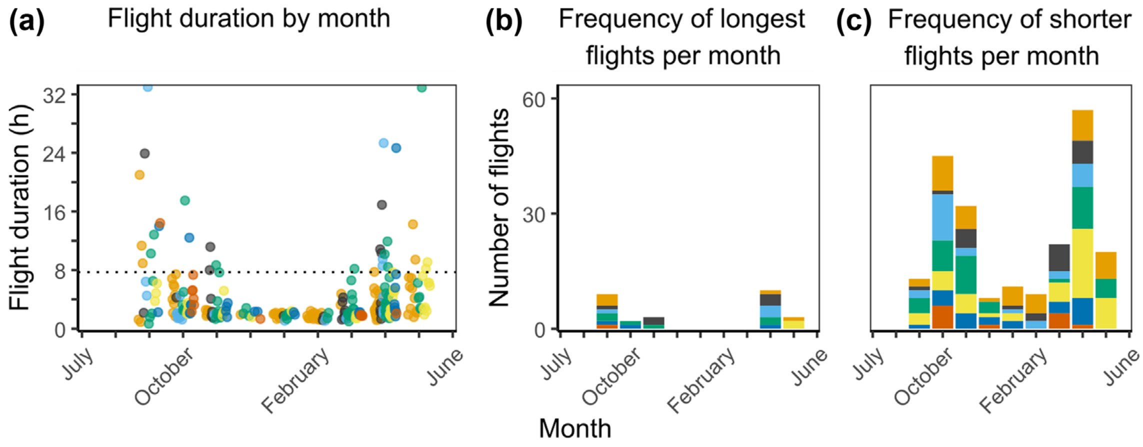

Figure 2. Scheduling and duration of snow bunting flights across the annual cycle. (a) The duration of flights started in each month. The dotted line at 7.72 h illustrates the 90% quantile for flight duration and delineates between longest and shorter flights. (b) The frequency of longest flights started during each month. (c) The frequency of shorter flights started during each month. Only the first annual cycle is depicted for birds with two annual cycles recorded, and data from the months June to August were excluded because these months represent the breeding season (see 'Material and methods'). Each color represents a different bird ID.

predictor day of the year (defined below) and the two-level categorical predictor activity phase ('active', 'inactive') using a linear mixed-effects model (LMM) with bird ID nested within annual cycle as a random intercept. We expected phase duration to be circular and follow an approximately 365-day period. We therefore transformed the circular predictor day of year into two linear variables by converting the day of the year to radians and including the sine and cosine of the radian as continuous predictor variables in the model (Cox 2006, Huffeldt et al. 2021b). Both the sine and cosine of day of year interacted with activity phase in the model.

For all models, to test whether predictors explained a significant amount of variation, we compared models to a relevant intercept only, 'null', model using a likelihood ratio test (Tredennick et al. 2021). We identified statistical significance of models at significance level alpha = 0.05. For significant models, we reported model estimated marginal means and 95% CIs of model predictions calculated using the 'emmeans' R-package (Lenth 2023). If nested random effects in a mixed-effects model explained very little ($< 1.0 \times 10^{-9}$) to no variation, they were unnested and included as separate random effects in the model. If a random effect explained very little to no variation, then the random effect was dropped, and we used (G)LMMs, linear models (LM), or generalized linear models (GLM), as appropriate. We checked model assumptions using the 'DHARMa' R-package (Hartig 2022) and visually assessed histograms of residuals. We used the 'glmmTMB' R-package (Mollie et al. 2017) for all mixed-effects models.

Analyses of flights

To understand how snow buntings scheduled their flights across the diel cycle, we used a suite of five models to test different relationships. We first modeled the proportion of all flights that were initiated in each phase using generalized linear mixed-effects models (GLMM) with binomial error structures as a function of the interaction of flight initiation phase (categorical predictor: 'active', 'inactive', and 'transition') and flight duration category (categorical predictor: 'longest', 'shorter'), including bird ID as a random intercept to account for repeated measures. We repeated this GLMM analysis for only the longest and only the shorter flights, by using similar models that included the proportion of either longest or shorter flights initiated during the three phases as a response variable and the flight initiation phase as the only predictor.

We then tested whether the mean duration flown during the active and inactive phase differed for longest and shorter flights, to better understand how snow buntings scheduled flights. We built a GLMM with a Tweedie error structure, flight duration during the active and inactive phase per flight as a response variable, and an interaction between flight duration category and the flight phases 'active' and 'inactive'. Duration flown during the transition phase was excluded from these analyses, as we wanted to get an idea of activity during presumed active and inactive phases only. We used bird ID nested within annual cycle as a random intercept to account for repeated measures.

To identify whether flight initiation phase predicted flight duration, we also built a LMM. Flight duration was a continuous response variable and was log-transformed before modelling. The flight initiation phase ('active', 'inactive', and 'transition') was a categorical predictor. We used bird ID nested within annual cycle as a random intercept to account for repeated measures.

Results

Diel activity rhythms and phases

Male snow buntings maintained strong diel activity rhythms with a 24-h period across the full annual cycle, including during polar day (Fig. 3, Table 1). The only exception was during the longest migratory flights (Fig. 3, Supporting information), and only in April did migratory flights disrupt robust 24-h periodicity (mean period = 26.68 ± 7.83 h; Table 1). The duration of the active and inactive phases changed across the annual cycle with a 365-day period (LMM: $\chi^2_5 = 4962.00$, $p < 0.0001$; Fig. 4). The duration of the active phase ranged from a mean of 17.92 ± 1.02 h (median = 17.90 h) during June to 9.79 ± 0.90 h (median = 8.33 h) during December (Table 2). The duration of the inactive phase had an inverse relationship to the active phase and ranged from 5.87 ± 1.07 h (median = 6.15 h) during June to 14.23 ± 0.94 h (median = 15.62 h) during December (Table 2). The inactive phase became longer than the active phase from approximately October through February (Table 2, Fig. 4).

Flight duration and annual scheduling

Ninety percent of flights were less than 7.72 h, and the 10% of flights ≥ 7.72 h occurred mainly during months associated with migration: April, May, September, October, and November (shorter flights: n = 274; longest flights: *n* = 31; Fig. 2). The seven snow buntings undertook a mean ± SD of 30.44 ± 11.51 (median = 27; range = 12 to 47) shorter flights and 3.44 ± 1.94 (median = 3; range = 1 to 6) longest flights per individual per annual cycle (Fig. 2). The mean duration of shorter flights was 2.80 ± 1.52 h (median = 2.25 h; range = 0.67 to 7.67 h), while the mean duration of longest flights was 13.99 ± 7.14 h (median = 11.17 h; range = 7.75 to 33.00 h). Although we could not identify the specific migration routes of the snow buntings in our study, the longest flights occurred in months when we expected the buntings to cross the Barents Sea (Fig. 2) and the birds overwintered in the steppes of western Siberia (Supporting information). Combined, this suggested that the birds used the study population's previously described migration route and overwintering area (Snell et al. 2018).

Flights in relation to diel activity rhythms

Most flights were shorter and began during the active phase (46%), while another approximately 26% of flights were shorter and initiated during the inactive phase (GLM: $\chi^2_5 = 330.98$, $p < 0.0001$; Table 3, Fig. 5a). By definition 10% of flights were longest, and an estimated 55% of these longest

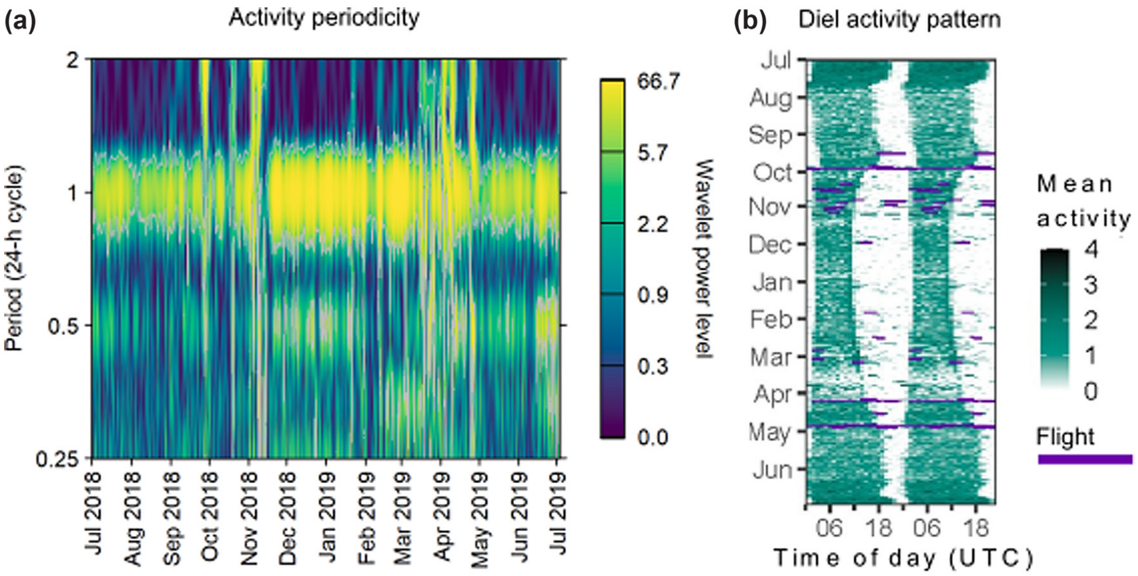

Figure 3. Diel activity rhythm and flights across the annual cycle in the snow bunting. (a) An example of a wavelet power spectrum illustrating the periodicity of snow bunting X0AC's activity. Warmer colors (yellow to lime green) surrounded by a grey border indicate significant periodicity at alpha = 0.05. Month ticks are the first of each month. Wavelet power is related to the strength, or amplitude, of the periodic signal. (b) A double-plotted actogram illustrating the mean activity level per hour and flights of X0AC. Data from the months June to August were excluded for flight analyses. See the Supporting information for wavelet power spectra and actograms for all individuals.

flights began during the transition phase, while the proportions of longest flights initiated during the active and inactive phases were not statistically different (GLM: $\chi^2_2 = 9.84$, $p = 0.007$; Table 3, Fig. 5b). For each longest flight, individuals flew 2.65 h more during the inactive phase compared to the active phase (GLM: $\chi^2_3 = 155.12$, $p < 0.0001$;Table 4, Fig. 6). About 52% of the shorter flights began during the active phase, while about 29 and 19% began during the inactive and transition phases, respectively (GLM: $\chi^2_2 = 66.72$, $p < 0.0001$; Table 3, Fig. 5c). During shorter flights, snow buntings flew 0.26 h more during the active, compared to the inactive, phase (Table 4, Fig. 6).

The phase in which flights were initiated predicted the flight duration (LM: $\chi^2_2 = 23.08$, $p < 0.0001$; Table 5). When considering all flights in a single analysis, the mean duration of flights that initiated during the active phase was 2.45 h (Table 5, Fig. 7). Flights initiated during the transition and inactive phases were longer than those initiated during the active phase and averaged 3.78 and 3.24 h, respectively (Table 5, Fig. 7).

Discussion

The male snow buntings maintained 24-h periodicity in activity throughout the year (Fig. 3, Table 1), which provides empirical support for the hypothesis that polar breeding songbirds maintain diel rhythms across the annual cycle. The only deviation from robust 24-h periodicity was in April where presumptive migratory flights (i.e. longest flights) caused a mean period of 26.68 h (Fig. 2–3, Table 1), although the median period (23.97 h) was still close to 24 h and the 95%

Table 1. Monthly periodicity of activity rhythms of snow buntings estimated using Lomb–Scargle periodogram analysis. April is in italics to indicate when the robust diel activity rhythm attenuated, but the 95% CI still overlaps 24 h and the median is near 24 h, indicating a marginal deviation. SD = standard deviation. PN_{max} = the test statistic for Lomb–Scargle periodogram analysis.

Month	Period (h) (mean ± SD)	Median (h)	Period (h) 95% CI	PN_{max} (mean ± SD)	n individuals	n months
July	23.85 ± 0.14	23.83	23.72 to 23.98	0.31 ± 0.03	7	11
August	24.1 ± 0.06	24.12	24.05 to 24.16	0.47 ± 0.02	7	9
September	23.98 ± 0.10	23.97	23.89 to 24.07	0.15 ± 0.05	7	9
October	23.99 ± 0.11	23.97	23.89 to 24.09	0.30 ± 0.09	7	9
November	23.92 ± 0.12	23.97	23.81 to 24.03	0.22 ± 0.10	7	9
December	23.97 ± 0.00	23.97	23.97 to 23.97	0.46 ± 0.09	7	9
January	23.97 ± 0.00	23.97	23.97 to 23.97	0.52 ± 0.06	7	9
February	23.96 ± 0.0004	23.96	23.96 to 23.96	0.44 ± 0.04	7	9
March	23.95 ± 0.07	23.97	23.88 to 24.01	0.28 ± 0.13	7	9
April	*26.68 ± 7.83*	*23.97*	*19.44 to 33.92*	*0.20 ± 0.16*	*7*	*9*
May	23.98 ± 0.17	23.97	23.80 to 24.16	0.23 ± 0.14	6	8
June	24.01 ± 0.05	24.01	23.96 to 24.06	0.28 ± 0.04	6	8

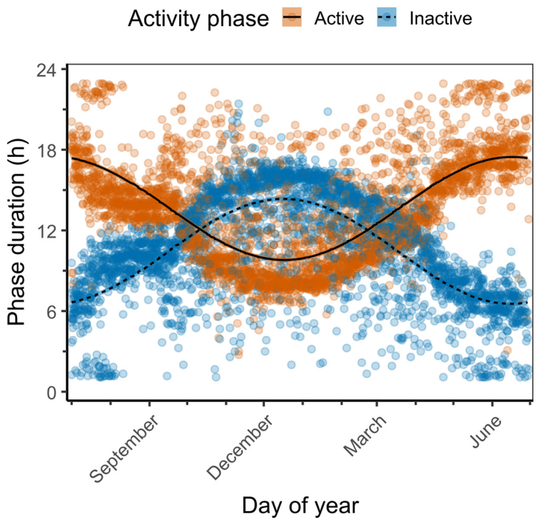

Figure 4. Change in duration of the active and inactive phase of the snow bunting's diel activity rhythm across the annual cycle. Colored points are individual data points. Black lines and colored shaded areas are estimated marginal means and 95% confidence intervals, respectively, from the significant model (LMM phase duration ~ sine(2 × π/365 × day of year) × activity phase + cosine(2 × π/365 × day of year) × activity phase + (1| annual cycle) + (1 | bird ID): $\chi^2_5 = 4962.00$, $p < 0.0001$).

CI (19.44 to 33.92 h) still overlapped 24 h, indicating a marginal and non-statistically significant deviation from a 24-h period. The apparent drift in activity across days in August and September does not result in deviation from 24-h periodicity (Table 1, Fig. 3, Supporting information) and so does not indicate free-running rhythms. Instead, we suspect that the activity onset during the two months tracks the morning shift in the diel cycle of solar altitude at these high latitudes, while still maintaining 24-h periodicity (Table 1). Lapland longspurs, willow warblers, and northern wheatears, the only other songbirds, to our knowledge, investigated using a variety of different methods within their natural range near polar latitude, also appear to maintain 24-h activity rhythms that align with the diel cycle (Asbirk and Franzmann 1979, Silverin et al. 2009, Ashley et al. 2013, 2014), which supports the snow bunting results, but contrasts with many non-passerines (Reierth and Stokkan 1998, Lesku et al. 2012, Steiger et al. 2013, Huffeldt et al. 2021a) and mammals (van Oort et al. 2007, van Beest et al. 2020; c.f. Williams et al. 2017) that do not express these organized diel activity rhythms during the continuous light of polar day. In the case of the Lapland longspurs, circadian rhythms control the expression of diel activity (Ashley et al. 2014), suggesting that the circadian system underlies the maintenance of a diel periodicity during polar day in songbirds and probably facilitates the temporal organization of homeostatic processes (Williams 2015). Additionally, because circadian rhythms are implicated in properly functioning circannual rhythms and photoperiodism (Gwinner 1986, Appenroth et al. 2021), maintaining functional diel rhythms driven by the circadian system probably facilitates scheduling annual phenological transitions.

The male snow buntings did not strictly schedule all flights to either their active or inactive phase of their dominant diel activity rhythm, indicating that not all migratory songbirds schedule the initiation or execution of their flights to a specific phase of their diel activity rhythm. Instead, snow buntings flexibly scheduled their flights depending on the duration of the flight, which was more similar to the Eurasian hoopoe *Upupa epops* than some other songbirds (Adamík et al. 2016, Briedis et al. 2020). The snow buntings scheduled the initiation of approximately 46 and 26% of their shorter flights during their active and inactive phase, respectively (Fig. 5, Table 3). Despite a 20% difference in whether shorter flights began during their active or inactive phase, snow buntings spent only a difference of 0.26 h flying between these phases for shorter flights (Fig. 5, 6, Table 4). Contrasting these shorter flights, the longest flights ≥ 7.72 h began primarily during the transition between their active and inactive phases of their activity rhythm (Fig. 5, Table 3), suggesting take-off during the diel transition between high and low light intensities typical of sunset, if we assume that snow buntings are generally active diurnally or when light intensity is high (Fig. 3, 4). The longest flights initiating around sunset would be similar to another previously assumed diurnal migrant, the tawny pipit *Anthus campestris*, which after tracking with

Table 2. Monthly duration of the active and inactive phases of snow buntings' diel activity rhythm.

	Active phase			Inactive phase		
Month	Duration (h) (mean ± SD)	Median (h)	95% CI (h)	Duration (h) (mean ± SD)	Median (h)	95% CI (h)
July	16.57 ± 1.03	15.88	15.62 to 17.53	7.23 ± 1.20	7.92	6.12 to 8.34
August	14.33 ± 0.44	14.08	13.92 to 14.73	9.70 ± 0.43	9.92	9.30 to 10.10
September	14.60 ± 0.40	14.17	14.23 to 14.97	9.65 ± 0.41	10.00	9.27 to 10.04
October	12.01 ± 0.90	11.21	11.18 to 12.85	12.26 ± 0.94	13.58	11.39 to 13.13
November	10.66 ± 0.50	9.38	10.20 to 11.12	13.50 ± 0.62	14.92	12.93 to 14.08
December	9.79 ± 0.90	8.33	8.95 to 10.62	14.23 ± 0.94	15.62	13.36 to 15.10
January	10.03 ± 0.85	8.75	9.25 to 10.81	13.93 ± 0.85	15.25	13.14 to 14.72
February	11.52 ± 0.74	10.54	10.84 to 12.20	12.48 ± 0.71	13.25	11.82 to 13.13
March	13.32 ± 0.56	12.50	12.80 to 13.83	10.75 ± 0.53	11.75	10.27 to 11.24
April	14.49 ± 2.05	14.92	12.59 to 16.38	9.64 ± 1.37	9.21	8.37 to 10.91
May	17.56 ± 1.03	16.83	16.48 to 18.64	6.64 ± 0.91	7.08	5.68 to 7.59
June	17.92 ± 1.02	17.90	16.85 to 18.99	5.87 ± 1.07	6.15	4.75 to 6.99

Table 3. Proportion of all flights (a), only longest flights (b), and only shorter flights (c) initiated during different phase of the snow bunting's diel activity rhythm. For each dependent variable (a-c), rows with different superscript letters after the 95% confidence interval (CI) are statistically different from each other. Mean proportions are estimated marginal means from significant models, (a) GLM proportion of all flights ~ flight initiation phase × flight duration category: $\chi^2_5 = 330.98$, $p < 0.0001$; (b) GLM proportion of longest flights ~ flight initiation phase: $\chi^2_2 = 9.84$, $p = 0.007$; (c) GLM proportion of shorter flights ~ flight initiation phase: $\chi^2_2 = 66.72$, $p < 0.0001$.

Flight initiation phase	Flight duration category	Mean proportion	SE	95% CI
(a) All flights				
Active	Longest	0.020	0.008	0.009 to 0.043 ^{a}
Transition	Longest	0.056	0.013	0.035 to 0.088 ^{b}
Inactive	Longest	0.026	0.009	0.013 to 0.052 ^{a}
Active	Shorter	0.46	0.028	0.41 to 0.52 ^{c}
Transition	Shorter	0.17	0.022	0.14 to 0.22 ^{d}
Inactive	Shorter	0.26	0.025	0.22 to 0.31 ^{e}
(b) Longest flights only				
Active		0.19	0.071	0.090 to 0.37 ^{a}
Transition		0.55	0.089	0.37 to 0.71 ^{b}
Inactive		0.26	0.079	0.13 to 0.44 ^{a}
(c) Shorter flights only				
Active		0.52	0.030	0.46 to 0.57 ^{a}
Transition		0.19	0.024	0.15 to 0.25 ^{b}
Inactive		0.29	0.028	0.24 to 0.35 ^{c}

multisensor data loggers, appears to be primarily a nocturnal migrant (Briedis et al. 2020). During these longest flights, the buntings spent 2.65 h more time flying during their inactive phase than their active phase (Fig. 6, Table 4), despite the inactive phase being shorter than the active phase in most months containing their longest flights (Table 2, Fig. 2, 4). This result suggests a preference for nocturnal migration when flying for long durations (Fig. 3), probably associated with the obligate endurance flight crossing the Barents Sea or other ecological barriers (Snell et al. 2018). Our results using high-resolution activity logging align with the snow bunting's presumptive migration strategy consisting of mainly short (potentially nomadic) flights and only a few long flights to cross barriers (Snell et al. 2018), and support historical accounts that snow buntings probably migrate during both day and night (Parmelee 1968, Montgomerie and Lyon 2020).

Foundational experiments on avian circannual rhythms and migration demonstrated that the diel phase of migration is endogenously controlled and hardwired as part of the migratory program (Gwinner 1977, 1986, Stey et al. 2017, Åkesson and Helm 2020), and, in many cases, the only deviation from the endogenous phase relationship between a 24-h activity rhythm and the diel cycle occurs during barrier crossings requiring extended flights (Adamík et al. 2016, Ouwehand and Both 2016, Liechti et al. 2018, Norevik et al. 2023).

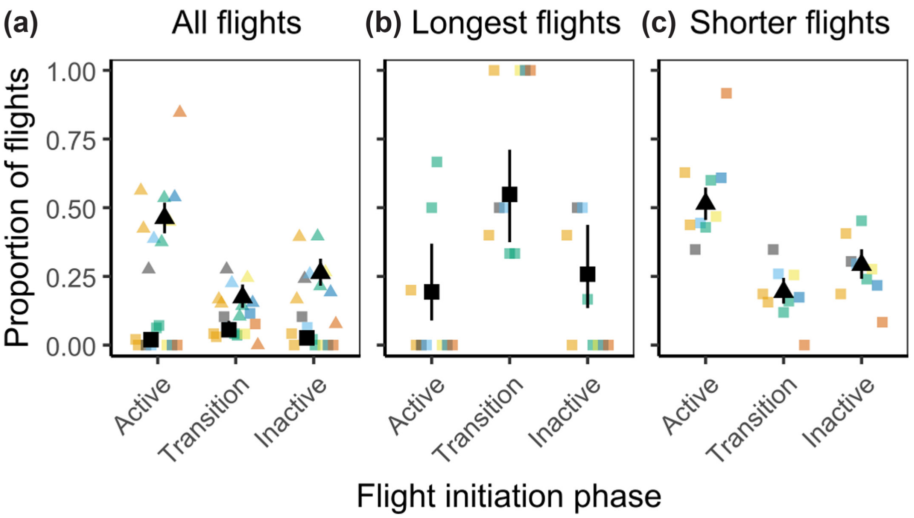

Figure 5. Proportion of snow bunting flights initiated during the different activity phases. (a) The proportion of all longest (≥ 7.72 h, squares) and shorter (< 7.72 h, triangles) flights initiated during phases of the diel activity rhythm. (b) The proportion of longest flights initiated during phases of the diel activity rhythm. (c) The proportion of shorter flights initiated during phases of the diel activity rhythm. For all panels, each color represents a different bird ID, and large black points and vertical lines are estimated marginal means and 95% confidence intervals, respectively, from significant models (Table 3).

Table 4. Mean duration flown during the active or inactive phase of snow bunting's of longest and shorter flights across their diel activity rhythm. Rows with different superscript letters after the 95% confidence interval (CI) are statically different from each other. Durations are estimated marginal means from the significant model, GLM duration flown ~ activity phase × flight duration category: $\chi^2_3 = 155.12$, $p < 0.0001$.

Activity phase	Flight duration category	Mean duration (h)	SE	95% CI
Active	Longest	4.96	0.79	3.63 to 6.77 ^{a}
Inactive	Longest	7.61	1.05	5.80 to 9.97 ^{b}
Active	Shorter	1.37	0.11	1.17 to 1.61 ^{c}
Inactive	Shorter	1.11	0.10	0.93 to 1.32 ^{d}

Some songbirds, such as the snow bunting, however, may employ a migratory strategy spanning both the active and inactive phases of their diel activity rhythm (Adamík et al. 2016; Fig. 3, 5, 6), suggesting flexibility in alignment to a specific diel activity phase. Together, this suggests that snow buntings may have a flexible endogenous migratory program that allows flights to begin and continue independent of their predominant activity rhythm. Indeed, the proportion of longest flights that the snow buntings initiated during the active and inactive phases did not differ (in total 45% of all longest flights; Table 3). The snow bunting's propensity to fly the majority of their longest flights during their typical inactive phase (Table 4) and initiate the majority of their longest flights during the transition between the active and inactive phases (55% of all longest flights), however, suggests an ecological advantage for flying long durations during presumptive night (Alerstam 2009). The relationship of bird migration to the diel light–dark cycle and activity rhythms is an open area of research, with no systematic investigations, to our knowledge, about how migration parameters relate to diel migratory strategy.

Table 5. Durations of flights initiated during different phases of the snow bunting's diel activity rhythm. Rows with different superscript letters after the 95% confidence interval (CI) are statistically different from each other. Mean durations are estimated marginal means from the significant model, LM flight duration ~ flight initiation phase: $\chi^2_2 = 23.08$, $p < 0.0001$.

Flight initiation phase	Mean duration (h)	SE	95% CI
Active	2.45	0.13	2.20 to 2.72 ^{a}
Transition	3.78	0.30	3.24 to 4.41 ^{b}
Inactive	3.24	0.23	2.83 to 3.72 ^{b}

Another common assumption is that the solar day controls many diel rhythms and entrains most circadian rhythms (Pittendrigh 1993, Kumar 2017). However, snow buntings may be using the sidereal day instead of the solar day to track the diel cycle during parts of the year, because of the low variation around a mean period of approximately 23.9 h and because, in winter months, the 95% CI of periods does

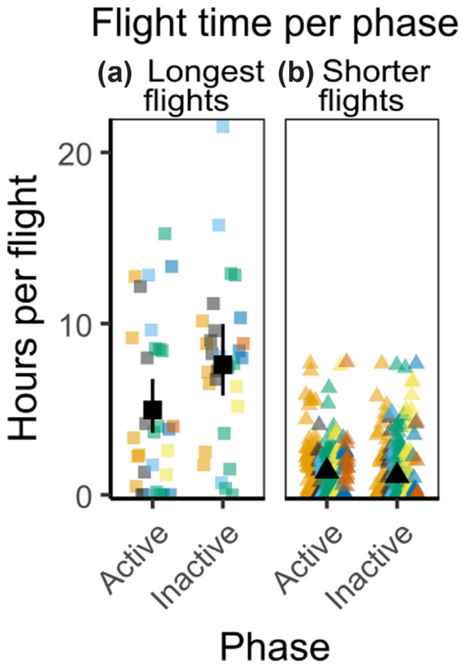

Figure 6. Duration of longest and shorter flights flown during the active and inactive phases. The duration flown during the active and inactive phases of the diel activity rhythm for each (a) longest (≥ 7.72 h, squares) and (b) shorter (< 7.72 h, triangles) flights. A single flight can overlap both the active and inactive phase, resulting in durations flown in a phase less than the 7.72 h threshold. Each color represents a different bird ID, and large black points and vertical lines are estimated marginal means and 95% confidence intervals, respectively, from the significant model (Table 4).

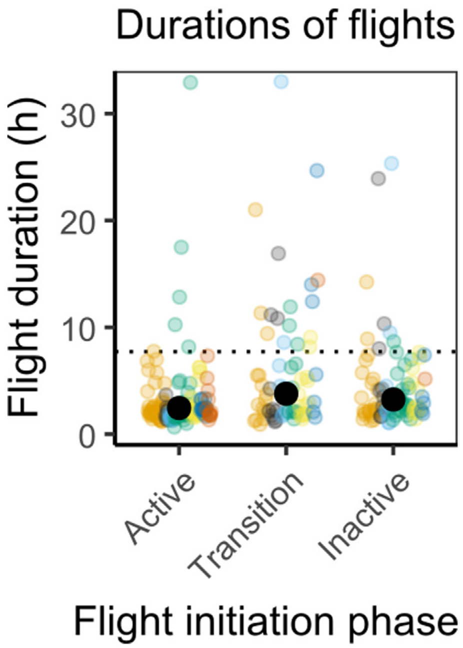

Figure 7. Duration flown per snow bunting flight. Duration of flights initiated during different phases of an individual's diel activity rhythm. The dotted line at 7.72 h illustrates the 90% quantile for flight duration and delineates between longest and shorter flights. Each color represents a different bird ID, and large black points and vertical lines are estimated marginal means and 95% confidence intervals, respectively, from the significant model (Table 5).

not overlap 24 h (Table 1). This remains highly speculative, because a solar day is only about four minutes longer than a sidereal day, and the 5-min resolution of our data may not ascertain which measure of a diel cycle snow buntings use to schedule their behavior. If snow buntings did use the sidereal day during some months, this would mean they tracked the diel cycle using different cues across the annual cycle. Despite being very speculative, we find this an intriguing possibility that can be tested with strictly controlled experiments that disentangle whether different measures of a day are used.

In conclusion, we found that male snow buntings scheduled flights flexibly across their otherwise robust 24-h activity rhythm that persists across the annual cycle, even during the continuous light of the polar summer. The flexible scheduling of migratory flights suggests that snow buntings can take advantage of beneficial conditions independent of time of day, although with our data it is not possible to identify which phase of the diel cycle activity or flights aligned with. Additionally, the result that most of the longest flights were flown during the inactive phase suggests an ecological advantage for longer flight times during night or otherwise diel phases with the lowest illumination, if we assume that snow buntings are generally diurnal (Parmelee 1968, Krüll 1976, Meltofte 1983, Montgomerie and Lyon 2020). The robust diel activity rhythms across the year infers an advantage of maintaining a 24-h activity rhythm aligned with the Earth's rotation, despite changes in the migratory and photic environments across the year. However, which celestial cues the snow buntings use to align their activity to the diel cycle across the year remains uncertain and requires additional investigation, while data from females are also needed to gain a comprehensive understanding of snow buntings' flight and activity schedule across the annual cycle.

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Author contributions

Nicholas P. Huffeldt: Conceptualization (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Frode Fossøy**: Funding acquisition (equal); Investigation (equal); Resources (equal); Writing – review and editing (equal). **Linus Hedh**: Formal analysis (supporting); Writing – review and editing (equal). **Arne Moksnes**: Investigation (equal); Resources (equal); Writing – review and editing (equal). **Katherine R. S. Snell**: Investigation (equal); Resources (equal); Visualization (supporting); Writing – review and editing (equal). **Bård G. Stokke**: Funding acquisition (equal); Investigation (equal); Resources (equal); Writing – review and editing (equal). **Christian Stolz**: Investigation (equal); Writing – review and editing (equal). **Kasper Thorup**: Funding acquisition (equal); Investigation (equal); Resources (equal); Writing – review and editing (equal). **Sissel Sjöberg**: Conceptualization (supporting); Data curation (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

The data and associated R script used are available from the Zenodo Repository: https://doi.org/10.5281/zenodo.17113061 (Huffeldt et al. 2025).

Supporting information

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

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