Diel and seasonal rhythmicity in activity and corticosterone in an Arctic migratory herbivore: A multifaceted approach

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Abstract

Birds that migrate from temperate areas to the Arctic for breeding lose their strongest *Zeitgeber* of circadian organization when they cross the Arctic circle in spring – the 24h geophysical light-dark cycle. Under continuous daylight various behavioural and physiological patterns have been detected in both free-ranging and laboratory animals. To better understand the evolution of plasticity in circadian clocks, it is essential to study behavioural and physiological rhythmicity in the context of a species' ecology. Employing a multifaceted approach, which included wildlife cameras, accelerometers, and non-invasive sampling of hormone metabolites, we investigated activity patterns and corticosterone rhythmicity in a migratory herbivore, the Svalbard barnacle goose (*Branta leucopsis*), during its Arctic breeding season. We detected that females showed a combination of both ultradian and diel rhythmicity in incubation recesses and sleep, respectively. In both parents, rhythms in activity continued over the period, when goslings were present. During moult, many geese aligned activity with the tidal rhythm. Barnacle geese showed weak diel rhythmicity in excreted corticosterone metabolites. This suggests that while Arctic geese may adopt an alternative *Zeitgeber* during the Arctic summer to keep a diel rhythm, ultradian rhythmicity is crucial and geese are able to tune their rhythms flexibly to environmental conditions.

Keywords

Camera trap, GPS transmitter, circadian rhythmicity, hormones, continuous daylight, polar

Introduction

Various biological processes occur rhythmically and are restricted to specific times of the day or season [1, 2], which in many species is maintained by using photoperiod, the environmental period of daylight, as a *Zeitgeber* [3]. Upholding these rhythms in polar regions is challenging insofar as above the Arctic and below the Antarctic circle (66°N and S) natural light is completely absent in winter but continuously present during the summer [4]. Nevertheless, various Arctic species are able to retain endogenous and behavioural rhythms [reviewed in 1, 5].

Arctic vertebrates show plasticity in rhythmicity in behavioural activity within individuals, between individuals and between species. Patterns may vary seasonally within individuals, *e.g.* driven by annual changes of day length [5, 6]. For example, the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), the sole permanent resident bird on Svalbard, exhibits ultradian activity patterns with periodic feeding during polar summer and winter days. In contrast, during spring and fall its activity patterns are diurnal and feeding mainly occurs within daylight hours [7]. Between individual differences exist, for example, in migratory, bi-parentally breeding shorebirds, where different conspecific pairs may show different incubation rhythms even in pairs which breed in the same area [5, 8]. Furthermore, Arctic vertebrate species are highly variable in their behavioural activity with some species (i) being completely *arrhythmic,* (ii) showing *circadian or diel rhythmicity, i.e.* displaying a recurring rhythm of approximately 24-hours even in the absence of light fluctuations, (iii) showing *ultradian cycles* of recurrent periods of foraging and resting bouts less than 24-hours, or (iv) showing *free running rhythmicity, i.e.* not synchronized with environmental time cues [1, 5]. For herbivore species, Bloch *et al*. suggested that ultradian activity patterns in polar regions are linked with feeding behaviour and digestive processes, because even at lower latitudes continuous activity is common in herbivores [6]. The diversity in behavioural responses to continuous daylight underline the plasticity of the circadian system and indicate the importance of life history and social contexts [5, 9].

Behavioural and physiological processes are regulated through the rhythmic excretion of hormones by an endogenous network of one or several 'Master' clocks, which then coordinate and synchronise more peripheral clocks [reviewed in 1, 2]. Crucial for tracking environmental cycles is

84 the neurohormone melatonin. Its diel secretion pattern, namely an extended peak at night and basal
85 secretion during the day, provides the paramount hormonal signal transducing day length for
86 peripheral clocks [3]. Melatonin secretion drives enduring changes in the hypothalamic-pituitary
87 adrenal axis (HPA), where low levels of melatonin culminate in the increased secretion of the adrenal
88 glucocorticoids. *i.e.* cortisol in mammals and corticosterone (CORT) in birds [1, 10, 11].
89 Glucocorticoids are involved in correlating peripheral clocks [12], are best known as one of the two
90 major stress response systems [13], and interrelate with feeding, modulation of energy storage and
91 mobilisation as well as activity [10]. They display robust diel rhythmicity in latitudes with year-round
92 day-night cycles [14-16, but see 17]. In temperate zones, the diel rhythmic pattern of baseline CORT
93 correlates with activity with low levels during inactive phases followed by a rise just before activity
94 begins, to remain high as long as birds are active [10]. In polar species with 24 hours of continuous
95 natural light during the summer, findings of a diel CORT rhythm are ambivalent, however. Common
96 murres (*Uria aalge*) maintain a diel CORT rhythm in the polar summer [18]. Contrary, the link
97 between activity, time of day and corticosterone was not evident in thick-billed murres (*U. lomvia*), a
98 species, which lacks the diel CORT rhythm [10]. Other such species without a diel CORT rhythm are
99 Adélie penguins (*Pygoscelis adeliae*) [4] and common eiders (*Somateria mollissima*) [19]. This
100 arrhythmicity was attributed to the suppression of melatonin secretion when photoperiod as *Zeitgeber*
101 is absent [5, 10, 19] and in common eiders it was linked to CORT interfering with the need to constant
102 forage [5], while in thick-billed murres it was ascribed to a stable modulation of energy storage and
103 mobilisation [10].
104 Many bird species, which show rapid migration to their Arctic breeding grounds, experience
105 large changes in light conditions en route, before they arrive in the polar regions with 24-hours of
106 continuous daylight. Latitudinal migrants may benefit from longer photoperiods at higher latitudes as
107 for diurnal animals daily activity and foraging time can be increased [20]. Nevertheless, such quick
108 fluctuations in light conditions present a significant challenge for circadian physiology [21-23]. There
109 is a surprising variation in the response of migrants to continuous daylight [*e.g.* 5, 8], despite that
110 changing to a different rhythm can be costly [24]. To increase our understanding of the evolution of
111 plasticity in circadian clocks in migratory birds, it is necessary to study rhythmicity in behaviour and

physiology in relation to the ecology of the species [*e.g.* 6, 8, 9].

Here we aim to quantify behaviour- and CORT-based rhythmicity in the barnacle goose, a migratory herbivore, during their breeding season in the Arctic using a multifaceted approach. Earlier findings on rhythmicity in barnacle goose behaviour and physiology are somewhat ambiguous. A recent study showed that barnacle geese lost diel rhythmicity in body temperature once they encountered continuous daylight during their migration to the Arctic breeding sites [23]. During incubation in the Arctic, however, a diel rhythm in incubation recesses was described earlier [25-27]. In addition, we showed that young barnacle geese retained a diel, albeit time-shifted, pattern of corticosterone metabolites (CORTm) determined from droppings, over one 24-hour period in their first summer [28]. Here, we investigated potential diel and seasonal rhythmicity in activity and daily excretion patterns of CORTm, using three different approaches; (i) activity and sleep, *i.e.* sleep posture of females indicative of sleep [29], during incubation were determined from wildlife camera photos placed in the vicinity of the nest, (ii) activity across the breeding season of females and males was assessed using data from accelerometers (ACC), and (iii) CORTm concentration was determined from individually assigned droppings. Contrary to mammalian herbivores, where digestive processes dictate ultradian activity patterns [30, 31], barnacle geese do not have complex digestive systems. Their summer food retention time is increased by interrupting feeding with longer loafing spells [30], however. We expect that barnacle geese may feed around the clock [*sensu* 23], which has been suggested to be a possible adaption of Arctic herbivores that allows for optimally utilizing the peak in food quality during the short summer [32]. As we predict ultradian rhythmicity in activity then to be important, thus, we expect to find no or only a weak diel rhythm of CORTm. In contrast, if barnacle geese strongly depend on an evolutionary-based endogenous clock to schedule their biology or respond directly to diel external cues, we expect diel rhythmicity in activity and CORTm throughout the breeding season, similarly to some other polar species [*e.g.* 18, 33, 34].

Materials and Methods

1. Study site and species

We collected data during the summers of 2020 – 2022 in a barnacle goose population nesting on islets in Kongsfjorden, Svalbard. Except on days with inclement weather when boating was not possible or polar bears (*Ursus maritimus)* were present, we monitored nests every other day during incubation and hatch on the two main breeding islands of the study area, Storholmen and Prins Heinrichøya from June to the beginning of July. We determined the exact nest location using a handheld GPS (Garmin GPSmap 64S), noted clutch size and identified parents by their individually recognizable engraved plastic leg rings when a researcher approached the nest [35]. To diminish disturbance, we got information on possible nests of geese with transmitters (see below) on other islands (Midtholmen, Juttaholmen, Observasjonsholmen) from colleagues who worked there regularly. Egg laying and incubation in barnacle geese takes approximately 29 days [36]. After hatching, many geese raise their goslings in or in direct vicinity of the village Ny-Ålesund (78°55′30″N 11°55′20″E) [37, 38]. Here, we observed geese at least twice-daily using binoculars or spotting scopes to identify individuals by their colour rings, to establish family size and record feather moult. From the first day of moult, the complete moulting process lasts 35 to 40 days on average, with a flightless period of ca. 25 days [39]. We used the flightless period from the first observation of loss of all flight feathers until 25 days later in our analyses (from now on called 'moult').

In 2020, we fitted one individual of 24 barnacle goose pairs (½ males and ½ females, sex based on cloacal inspection [35]) with black coloured OrniTrack-NL40 3G transmitter neckbands (Ornitela, UAB, Lithuania. Mass ~20 gram, height 21mm, diameter 38-40 mm). We caught ten geese on or near their nest on the islands Storholmen or Prins Heinrichøya during late incubation using two methods: (1) using an extendable pole with a small noose in fishing wire at one end, which was slid around the neck, quickly capturing the goose, or (2) by catching the geese by hand, which was mainly possible for aggressive males that came close. All remaining geese where caught during annually performed catches, during which flightless moulting geese are driven into corrals [30]. The 24 individuals were chosen following a suite of criteria, including that it would be desirable if both pair partners were

167 marked with unique colour rings previously (for details of criteria see [40]). During incubation, we
168 deployed three additional transmitters in 2021 and four in 2022.

169 **2. Activity during incubation and across the breeding season**

170 *I. Incubation patterns from wildlife camera photos*

171 To investigate rhythmicity over the period of incubation, we set up wildlife cameras (Usogood TC30
172 Trail Camera) from 9/6/2021 to 16/7/2021 near nests of incubating geese, which were fitted with GPS
173 transmitters in 2020 (n = 15). Cameras, set in time-lapse mode, took two pictures every five minutes.
174 We ultimately retrieved the cameras either after hatching or when a nest was predated or abandoned
175 [40].

176 We analysed pictures with Timelapse2 Image Analyser (version 2.2.4.3, [41]). We quantified
177 whether the female was (i) sitting on the nest, (ii) in 'sleep posture', *i.e.* head resting on back with
178 often beak tucked under wing [29], (iii) standing right next to the nest or (iv) absent from the nest (n
179 photos = 110739). For further analyses on nest recesses, we pooled behaviours (iii) and (iv) as *active*
180 and behaviours (i) and (ii) as *inactive*. For the analyses of 'sleep', we contrasted being in the sleep
181 posture with the other behaviours. Males sometimes nest sit [40], but here we focussed on females
182 only. Instances, where males nest sat, while females were on incubation recesses, were classified as
183 (iv) absent from nest.

184 In total, wildlife cameras supplied data from 2 hours to 20 days. We only used data which
185 exceeded the recommended minimum duration of ten days for biological rhythm analyses [42, 43].
186 We could assess activity, *i.e.* incubation recesses, and sleep patterns, from photos taken by the
187 wildlife cameras of 11 out of 15 females. The other four cases were discarded, because data were
188 insufficient due to nest (n = 2) or camera failure (n = 2).

189

190 *II. Seasonal activity from transmitter accelerometer data*

191

192 We used ACC data collected by the transmitters during the summers of 2021 and 2022 (2021: females
193 n = 8, males n = 9; 2022: females n = 9, males n = 9; same individuals across 2021 and 2022: n = 12).
194 When geese arrived within a geofence, *i.e.* a virtual boundary defined around a specific real-world
195 geographic area, that was put around their breeding area (rectangle latitude/longitude: top-left; 79.161
196 / 10.95, bottom-right; 78.737 / 13.131), the transmitters were set to record a GPS-fix every 15 min
197 when battery voltage was 75-100%, 30 min at 50-74%, 60 min at 25-49% or 240 min at voltages
198 lower than 25%. Immediately after each GPS-fix, a 2-sec ACC burst was taken at a frequency of 20
199 Hz. Gravitational acceleration was measured in unit g/1000 in the three spatial axes [44].
200 We used ACC data to identify activity and inactivity of individual geese during the breeding
201 season [45, 46]. For each goose, we checked the number of bursts taken during each GPS-fix to
202 ensure a complete dataset. Then, we calculated the vectorial sum of dynamic body acceleration
203 (VeDBA) from the ACC data, which is a proxy for energy expenditure [47]. For this, we first
204 calculated static acceleration, *i.e.* the average raw measured acceleration for each dimension (x, y, z)
205 within the bursts. Second, we subtracted the static acceleration from the raw data for each dimension,
206 thus getting dynamic acceleration. Last, we calculated the vectorial sum of dynamic body acceleration
207 of each burst by taking the square root of the summed dynamic accelerations of each dimension [47].
208 Following [46], we created probability density histograms to identify peaks for activity and inactivity
209 and used the *mix* function in the R-package *mixdist* to decompose the distribution into two gamma
210 distribution components for active and inactive behaviour [48]. We found the threshold between the
211 active and inactive behaviour distributions by calculating the intersection point between the two [Fig.
212 S1, 45, 46].
213 In addition, we estimated the nesting period based on the method described by [44] using
214 VeDBA and GPS data. Nesting is defined as the entire period of egg laying, nest building, incubation,
215 and hatching. For females, we took daily median VeDBA < 1 for motionless days, as this
216 corresponded best with observed periods of nesting (n = 14: nesting period or part of the nesting

period could be estimated, n = 3: nesting period could not be estimated due to transmitter attachment during hatching or when the goose was likely not breeding).

Most males, on the other hand, were never motionless during nesting (n = 14). Four males, however, did show motionlessness. The immobility of these males could plausibly be used to establish the nesting period. In addition, for nine males we established nesting period based on known nest location. For six males we could not establish nesting. In total, for 14 geese (males and females) we obtained both an observed nest location and an estimated nest location based on the transmitter data; the distance between these two was on average 2.37 meters (SD = 0.98, range 0.85 – 3.67, excluding an outlier of 25.45 meters where the handheld GPS was likely turned on too late).

Later breeding stages, *i.e.* when geese had goslings and were moulting, were based on observations (see above). For 13 geese we obtained data on the period with goslings, for 11 geese when they were moulting and for 3 geese that had goslings while moulting ('goslings & moult' period). Since these different breeding stages pose different demands on the geese [30], we tested for rhythmicity within these three periods. Once again, we only used data, which exceeded the recommended minimum duration of ten days for biological rhythm analyses. Therefore, we excluded four nesting periods, five gosling periods, one gosling & moult period and one moult period. We pooled the remaining two goslings & moult periods with the moult period data to increase sample size. For the gosling periods used in the analyses, goslings were observed until they were on average 27 days old. Because of limited sample size of geese with goslings due to high polar bear egg predation and Arctic fox (*Vulpes lagopus*) gosling predation, we did not take gosling age into account in our analyses.

3. Sample collection and corticosterone metabolite assay

To investigate diel rhythmicity of CORTm excretion, we collected droppings (faeces) of ringed geese in the village of Ny-Ålesund from 1/7/2020 to 13/8/2020 (n = 349 droppings. 26 individuals; 14 females, 12 males) and 16/6/2021 to 31/7/2021 (n = 333 droppings. 52 individuals; 28 females, 24 males). Of 17 individuals we collected samples in both years. We attempted to collect a minimum of three samples [49] per 3-hour time intervals, *i.e.* from 0:00 – 2:59, 3:00 – 5:59, …, 21:00 – 23:59 and

intended to cover one complete 24-hour cycle every week for each individual. This was not always possible, as pairs, which lost their offspring, sometimes left the area and could not be located. Logistically, collecting samples at a finer temporal scale from specific individuals proved not possible. Therefore, we were able to study diel patterns in CORTm only and could not determine possible ultradian patterns or changes in rhythmicity over the season. Only unambiguously assigned samples were collected and frozen at -20°C within 1 h (for methodology on how to collect droppings, see electronic supplementary material). Droppings were shipped frozen to the Dept. of Behavioural and Cognitive Biology, University of Vienna, Austria, for analyses.

Dropping samples (n = 679) for determining CORTm were quantified using an enzyme immunoassay validated for barnacle geese [50] and applied successfully in previous studies [*e.g.* 28]. Concentration limits ranged from 7.49 to 320.90 ng CORTm/g droppings (median concentration 32.13 ng/g) in 2020 and from 1.02 to 583.65 ng CORTm/g droppings (median concentration 28.56 ng/g) in 2021. Determined from homogenized pool samples, intra- and inter-assay coefficients of variation (% CV) were 11.91% (< 15%) and 13.03% (< 25%), respectively.

4. Statistical analyses

All analyses were performed in R version 4.4.0 (The R Foundation for Statistical Computing 2024).

I. Rhythmicity in activity

We plotted actograms to visualize overall activity patterns during incubation, as assessed from wildlife camera data, and across the entire breeding season as determined from transmitter data (*ggetho* package [51]). Actograms, which show rhythmicity or a lack thereof, were double-plotted to facilitate inspection. We tested for periodicity in actograms using Lomb-Scargle periodogram (LSP) analysis [*periodogram* function, *zeitgebr* package: 51, 52] during specific periods: *i.e*. the incubation period for wildlife camera data to the point when goslings hatched, and the nesting, gosling rearing and moult periods for the transmitter data. The LSP analysis was very suitable to discover periodicity

270 in our dataset, because it can handle unequally sampled time-series with missing data [52].
271 Periodicity, *i.e.* the regular recurrence of behaviour or an event over fixed, equal time intervals, is a
272 common but not universal trait of rhythmicity, which in itself emphasizes the repetitive pattern of
273 changes rather than precise timing [53]. We scanned the data at an oversampling rate of 100 to
274 distinguish periodicity between 1 and 18 hours to focus on ultradian rhythmicity, and between 18 and
275 36 hours to focus on diel rhythmicity [following 33, 43, 54]. Data were re-sampled every 5 minutes in
276 case of data from nest cameras and every 15 minutes for transmitter data. We used the *find_peaks*
277 function from the *zeitgebr* package to extract significant peaks ($p < 0.05$). Time-series data can
278 contain two separate peaks, which may point to a true combination of ultradian and diel rhythmicity
279 or it can be a data artefact [55]. We followed the methods of [54] to distinguish between these two: if
280 we found two peaks in the normalized power for the same individual with an 18 h window we
281 rejected the smaller peak if it was less than one-third the height of the larger one.
282 We investigated possible differences in ultradian and diel peak periods between breeding stages
283 (nesting, goslings and moult) using linear mixed-effects models (*lme* from the package *nlme,*[56, 57])
284 with peak period in hours as the response variable and breeding stage (categorical) as a predictor
285 variable. We controlled for the factor sex (categorical: female, male), the interaction between sex and
286 breeding stage and year (categorical). We accounted for repeated measures by adding ID as a random
287 effect. We used an automated model selection using the function *dredge* (package *MuMIn*) and AICc
288 [58]. We give the 95% confidence set of models in the electronic supplementary material [59] and
289 information including 85% confidence intervals for the full model in the text [60]. The 85% interval is
290 consistent with how variables are selected using AIC. When present in the top model, we computed
291 estimated marginal means for specific factors and comparisons among levels [package *emmeans*, 61].
292

293 *II. Diel patterns of immune-reactive corticosterone metabolites*

294

295 To investigate the association between predictor variables and CORTm concentration over the day,
296 we fitted linear fixed-effects models (*lme*). We log-transformed CORTm concentration to adhere to

297 model assumptions. The predictor variables in all models include time of day (continuous) and
298 controlled for year (categorical), day of the year (continuous) and sex (categorical). As time of day is
299 a circular variable, we changed it into two linear variables by first transforming hour of day to radians
300 and then calculating the sine and cosine of those radians. We included sine and cosine as continuous
301 predictor variables in our models [18, 62]. To account for repeated measures of the same individuals,
302 we added individual identity as random factor in all models. A more complex random slope model
303 could not be explored, because this fitted mixed model was singular. As above, we used model
304 selection using the function *dredge* (package *MuMIn*) and AICc and give the same model information.
305

306 **Results**

307 **5. Rhythmicity in activity**

308 *I. Rhythmicity during incubation*

309

310 All females showed rhythmicity in incubation recesses (Figure 1A, for actograms of all females see
311 electronic supplementary material Figure S2). Ten females showed a combination of both ultradian
312 and diel rhythmicity while one female showed ultradian rhythmicity only (electronic supplementary
313 material Table S1, Figure S3). The mean ultradian period in incubation recesses was 3.21 h (95% CI:
314 2.41, 3.89) and the mean diel period was 24.03 h (95% CI: 23.73, 24.38). Most incubation recesses
315 occurred during the conventional day (Figure 1B). In addition, nine females had both ultradian and
316 diel rhythmicity when resting in a sleep posture (Figure 1C, for actograms of all females see
317 electronic supplementary material Figure S4), while two females showed diel rhythmicity only
318 (electronic supplementary material Table S2, Figures S5). The mean peak ultradian period was 8.17 h
319 (95% CI: 5.14,10.64) and the diel period was 24.96 h (95% CI: 23.57,1 26.12). Overall, geese were
320 more often observed in the sleeping posture during conventional night time (Figure 1D).
321

322 *II. Seasonal rhythmicity in activity*

323 We detected rhythmicity in all geese over the course of the entire breeding season (for examples of
324 actograms of two individuals see electronic supplementary material Figure S6). With the exception of
325 three females, that showed no rhythmicity in activity patterns during nesting in 2022, most geese
326 showed diel rhythmicity or a combination of ultradian and diel rhythmicity during nesting and when
327 they had goslings (Figure 2 left and centre panel). Furthermore, we also detected either ultradian
328 rhythmicity only or a combination of ultradian and diel rhythmicity during moult (Figure 2 right
329 panel). We found evidence that breeding stage correlated with ultradian peak rhythmicity, as this
330 variable was present in all models within the 95% confidence set (Table 1A, electronic supplementary
331 material Table S3). The top model included breeding stage only (Table 1A) and post-hoc testing
332 revealed that the ultradian peak period during moult was significantly higher than when geese nested
333 or had goslings (Figure 3, goslings – moult; estimate = -6.05, SE = 1.75, p = 0.015, goslings – nesting;
334 estimate = 0.35, SE = 1.80, p = 0.9794, moult – nesting; estimate = 6.40, SE = 1.49, p = 0.004). There
335 was no strong indication that breeding stage influenced diel peak period, with the top model being the
336 null model (Table 1B, Figure 3, see also electronic supplementary material Table S4). The fraction of
337 time when the geese were active, varied between males and females during nesting, with females
338 being more active around noon while males were less active during that time (Figure 4A). When
339 geese had goslings or were moulting, females and males did not differ in the fraction of time active
340 (Figure 4B & C). During the period geese had goslings, there was a sharp decrease in activity after
341 midnight until early morning. This pattern was not present during moult.

342 **2. Diel patterns of immune-reactive corticosterone metabolites (CORTm)**

343

344 Our results revealed that CORTm concentration was marginally influenced by time of day (Table 2),
345 with both cosine and sine of time of day being present in the top model as well as in many models
346 within the 95% confidence set (electronic supplementary material Table S5). CORTm concentration
347 increased during conventional night time and decreased during day time hours (Figure 5). CORTm
348 concentrations were slightly different between the years (Table 2; 2020 median: 32.13 ng/g dropping,

range: 7.49 – 320.9 ng/g; 2021 median: 28.56 ng/g dropping, range: 1.02 – 583.56 ng/g). In addition, over the course of the season CORTm concentration slowly declined (Table 2). Collected mostly late at night on one specific day, several samples contained very high levels of CORTm, *i.e.* >200 ng CORTm/g droppings (n=7). Omitting these data points in a second analysis revealed that the outcome did not differ substantially, except that the top model now only included the cosine of time of day and year (electronic supplementary material Tables S6, S7).

Discussion

Svalbard barnacle geese maintain rhythmicity in physiology and behaviour during their Arctic breeding season. We detected that most females showed a combination of both ultradian and diel rhythmicity in incubation recesses and sitting in a sleep posture on the nest, respectively. Most females and males also showed a combination of ultradian and diel rhythmicity or only diel rhythmicity in activity, either when they were nesting or had goslings. Geese displayed either ultradian rhythmicity only or a combination of ultradian and diel rhythmicity in activity during moult, suggesting the adoption of a tidal rhythm. We detected no differences in peak periodicity between females and males across the various breeding stages. However, during the nesting phase, females and males exhibited contrasting activity patterns, with females leaving their nest more often during the day and males being more active during the conventional night. Furthermore, the geese showed weak diel rhythmicity in excreted corticosterone metabolites with concentrations increasing during the night and decreasing during the day.

Our results indicate the importance of ultradian rhythmicity in activity behaviour over the breeding season, but also the preservation of diel rhythmicity despite the continuous daylight of the Arctic summer. During nesting and when geese had goslings, they showed ultradian activity rhythms with a period of ~ 5 h (Figure 3). This ultradian rhythm might display a foraging activity – resting pattern, as is also shown by other Arctic herbivores such as Svalbard ptarmigan, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and muskoxen (*Ovibos moschatus*) during the summer solstice [*e.g.* 43, 54, 63, 64]. Such an activity pattern could be endogenously generated by ultradian oscillators [64] or controlled by the interplay of feeding and digestion [6, 65]. In addition, many geese showed

377 diel activity patterns in behaviour throughout the breeding season. The presence of a diel rhythm does
378 not inherently imply, however, that circadian systems are functional and/or entrained as the geese
379 could be reacting directly to external cues, also known as "masking" [1, 66]. For example, during
380 nesting female geese could respond adaptively to temperature differences between conventional day
381 and night, with slightly higher temperatures during the day despite 24h daylight. This might limit egg
382 cooling rates during incubation recesses, as shown in snow geese [*Anser caerulescens*, 67]. Males do
383 not incubate, although they sometimes sit on the nest [40], but often stand guard close by the nest
384 when the female is on incubation recesses [27]. Nests, however, are more vulnerable to predation if
385 the female is on recess [68] with the most significant egg predators, glaucous gulls (*Larus*
386 *hyperboreus*) and Arctic skuas (*Stercorarius parasiticus*), being more active during daytime [25].
387 This conflicts with females being on recesses then. Arctic foxes, on the other hand, are usually more
388 active at night [25, pers. obs.]. For more than a decade, however, no foxes have been observed on
389 those islands, where nests were monitored (pers. obs.). By contrast, foxes have been present in the
390 gosling rearing areas during the study years. Here, males and females usually rested close to water
391 bodies, into which they could escape to be safe from the fox [38, pers. obs.]. Although barnacle geese
392 may not be able to protect their nest against foxes even in the presence of both parents [69, 70], it was
393 suggested that fox predation might be the selective force of the observed diel rhythmicity during
394 incubation [25], *i.e.* a 'ghost of competition past'. If the day-active behaviour of female geese during
395 nesting is shaped by an expected daily rhythm in fox predation risk, it suggests the activity pattern is
396 regulated by an endogenous, innate circadian mechanism [71]. It is feasible that the geese' circadian
397 clock continues to function by employing alternative potential *Zeitgeber*s, such as diurnal changes in
398 light intensity, polarization patterns, solar azimuth, UV radiation, changes in the spectral composition
399 of light or slight changes in ambient temperature, which exist under polar summer conditions [72].
400 Studies on sleep patterns under natural conditions are rare due to challenges measuring this
401 behaviour in wild free-moving animals [73]. During incubation, we scored sleep posture, which has
402 been associated with rapid eye movement (REM) sleep and non-REM (NREM) sleep in domesticated
403 geese [29]. Sleep being scattered over the course of the day during summer has also been detected in
404 captive barnacle geese under a natural day - night cycle [74]. The authors proposed that barnacle

405 geese might have an attenuated circadian organization and may profit from becoming arrhythmic
406 during the polar summer. However, we found no strong evidence of arrhythmia.
407 During wing moult, barnacle geese are most vulnerable to fox predation [68]. At times, when
408 goslings are still present, parents are forced to forage in areas with high quality food even during
409 moult, thereby risking higher predation [38]. When goslings are depredated, however, adults can retire
410 to areas with lower quality food, but higher safety, *i.e.* tundra lake shores with a mossy vegetation
411 [38]. Over the past years, we increasingly noticed moulting geese without young to utilize the
412 intertidal area to rest and/or forage on algae (pers. obs.). The ~ 12 h ultradian rhythmicity patterns of
413 geese during moult reflect the falling and rising tides (Figure 3, electronic supplementary material
414 Figure S6A, [75]). The tides pose a constraint on an all-day-activity [76, 77], but the nearby sea
415 provides safety from foxes and the enhanced digestion during moult might also allow the geese to
416 utilize most of this food source, which is likely difficult to digest [31, 78]. Although geese were
417 shown to avoid salt-marsh vegetation in spring because presumably they are less capable
418 physiologically to cope with high salt loads in their environment [79], moulting barnacle geese
419 foraged on algae in our study, possibly benefitting from fresh river water nearby. Moult in geese is
420 energetically costly, because they moult wing coverts, some body feathers and flight feathers
421 simultaneously. To compensate, geese become less active overall (Figure 4C, [39]). In contrast, geese,
422 which still lead young, seem to retain their activity rhythm throughout moult. This should be
423 investigated in the future, because in our data set sample sizes of geese with goslings are too small to
424 confirm this finding conclusively.
425 Besides rhythmicity in activity, geese also maintained an, albeit weak, rhythmic pattern of
426 excreted CORTm (Figure 5), similar to what we found in human-raised barnacle goslings over 24
427 hours [28]. Glucocorticoids are integral in providing physiological signals to regulate biological
428 rhythms in sync with daily environmental cycles linking with activity and feeding [11, 12]. During the
429 gosling period, when we collected the majority of samples for CORTm measurements, our finding
430 contradicts with this general assumption, because values dropped from conventional midnight to
431 being lowest around midday, when geese are most active. As we discussed in our earlier study [28],
432 increased fox activity at night, during the period when the goose families preferentially rest, could

433 have affected the CORTm rhythm. In sum, whether the attenuated rhythm in CORTm is sufficient to
434 regulate activity patterns and other functions during the polar summer or whether it plays only a
435 minor role in endogenous timekeeping [18] needs to be investigated in the future.

436 The use of a multifaceted approach in this study, combining behavioural observations via
437 wildlife cameras and accelerometers with corticosterone measurements, has allowed for a
438 comprehensive understanding of rhythmicity in barnacle geese during their Arctic breeding season in
439 24h daylight. We found that accelerometers are a suitable alternative for investigating activity, where
440 time consuming direct behavioural observations are difficult. They are a valid substitute also for
441 pictures obtained from wildlife cameras, where a multiplicity of photos need to be analysed in detail
442 afterwards. The peak period in activity of five females during incubation, identified from both wildlife
443 cameras and accelerometers corresponded very well, for example. With the exception of one female,
444 where we found diel rhythmicity retrieved from the ACC data, which was not detected in data from
445 the wildlife cameras, the ACC-based activity patterns gave reliable results in the other four
446 individuals, despite the slightly longer 15 min intervals of ACC measurements relative to the 5 min
447 intervals of subsequent photos (ultradian: camera data; mean = 3.5 h, SD = 1.7, ACC data; mean = 3.8
448 h, SD = 1.7. diel: camera data; mean = 23.8 h, SD = 0.7, ACC data; mean = 24.2 h, SD = 0.1), This
449 indicates that ACC-based data describe activity very reliably. This is supported by another study in
450 captive barnacle geese, which investigated sleep – wake rhythms. Here, activity measurements from
451 ACC data correlated well with patterns retrieved from electroencephalograms (EEG) [74]. Contrary to
452 our study, where ACCs were mounted in neck collars, these ACCs were head-mounted. They took
453 high-frequency measurements at a high sampling rate of 100 Hz, and could, thus, record even small
454 head movements, whereas data provided in our study are less fine-tuned, because they were collected
455 at a lower rate, *i.e.* every 15 min during 2-sec bursts of 20 HZ. Therefore, we cannot immediately
456 make the same inferences at present. In a future study, however, it should be possible to estimate
457 sleep from ACC data also in wild geese.

458 To summarize, over the course of their Arctic breeding season, barnacle geese show some degree
459 of plasticity in their daily rhythms. Such intra-individual shifts in rhythms between sexes and breeding
460 stages also exist in shorebirds [reviewed in 1, 5]. One possible explanation is that in barnacle geese

the circadian clock mechanism keeps ticking, but the control, which it exerts over behavioural output, is plastic and is applied only when it provides some advantage [1, 2]. Alternatively, the observed rhythms are not endogenously controlled and geese respond directly to environmental or social cues, such as temperature, predation pressure, tides and/or their mates' activity. To investigate individual plasticity and consistency in behavioural and hormonal rhythmicity, and their effects on fitness, are novel avenues for future work in this Arctic herbivore.

Ethics

The study conforms to Directive 2010/63/EU and was conducted under FOTS ID 23358 from the Norwegian Animal Research Authority and approved by the Governor of Svalbard (RIS ID 11237).

Declaration of AI use

As all but one author are none native English speakers, AI was occasionally used while writing to improve language and readability. AI was sometimes used as 'search engine' to find suitable code for graphics.

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713 **Tables**

714

715 *Table 1: Intercept and coefficient estimates from the full models investigating differences in (A) ultradian peak period in*
716 *hours and (B) diel peak period in hours with corresponding standard errors (SE), 85% Confidence intervals (lower, upper),*
717 *and if the variable was selected in the top AIC model.*

Variable	(A) estimate	SE	lower	upper	AIC top	(B) estimate	SE	lower	upper	AIC top
Intercept	7.30	2.42	4.11	10.49		24.03	1.12	22.52	25.53	
Breeding stage - moult	5.79	2.89	1.74	9.83	Yes	-2.26	1.62	-4.50	-0.03	No
Breeding stage - nesting	-2.18	2.96	-6.33	1.97	Yes	-0.43	1.29	-2.21	1.35	No
Sex - Male	-2.91	2.96	-6.82	0.99	No	-0.22	1.56	-2.32	1.89	No
Year - 2022	-3.53	1.93	-6.23	-0.84	No	-0.22	0.86	-1.39	0.96	No
Breeding stage - moult: sex - male	1.04	3.58	-3.97	6.05	No	3.84	2.21	0.79	6.89	No
Breeding stage - nesting: sex - male	4.49	3.82	-0.85	9.84	No	-0.22	1.80	-2.70	2.26	No

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720 *Table 2: Intercept and coefficient estimates from the full model investigating rhythmicity in log-transformed corticosterone*
721 *metabolite concentration with corresponding 85% CIs, and if the variable was selected in the top AIC model.*

Variable	estimate	standard error	lower	upper	AIC top
Intercept	5.03	0.45	4.38	5.67	
cosine	0.1	0.04	0.05	0.15	Yes
sine	0.06	0.04	0.003	0.11	Yes
sex - male	-0.08	0.09	-0.21	0.05	No
year - 2021	-0.2	0.06	-0.29	-0.11	Yes
year day	-0.007	0.002	-0.01	-0.004	Yes

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Figures

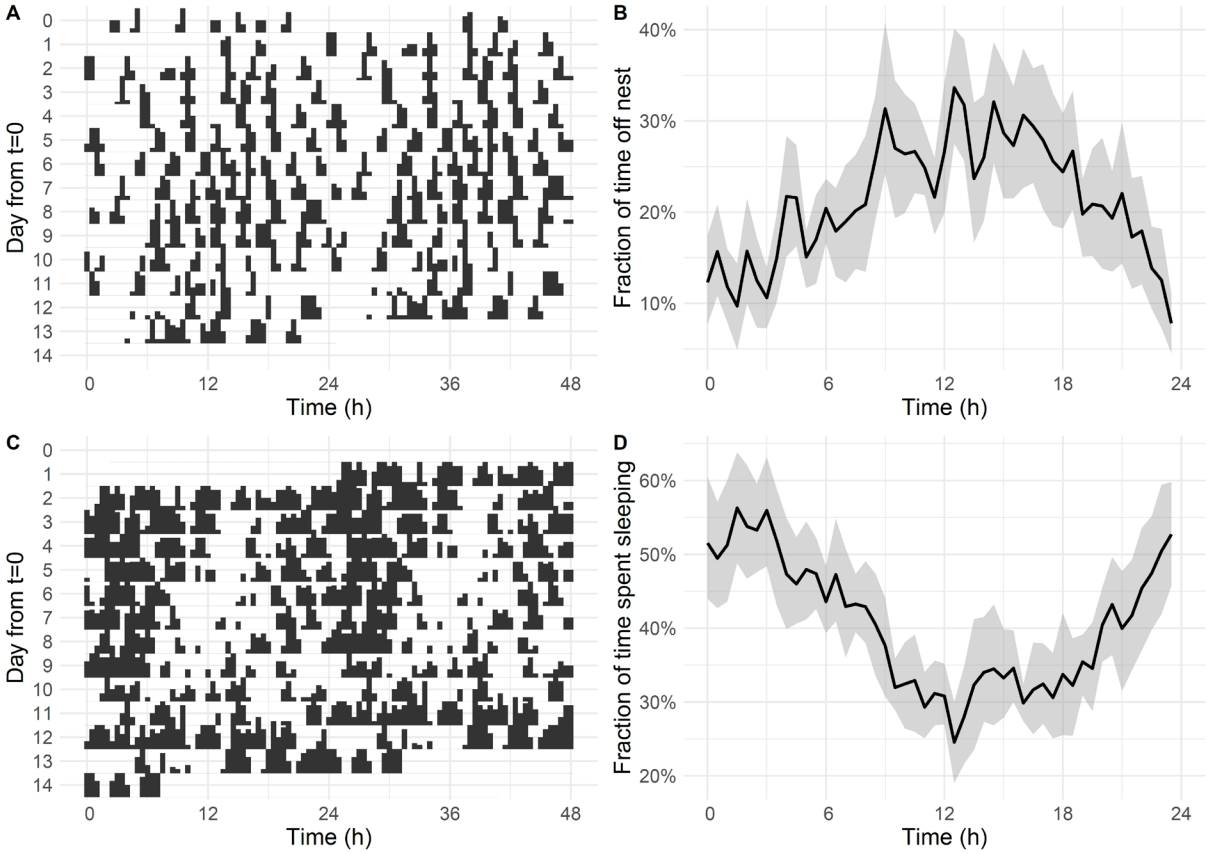

Figure 1: Rhythmicity of females during incubation recesses [panels (A) and (B)] and 'sleep' [panels (C) and (D)]. Double plotted actograms of female ID CA41113 as an example show in black when the female is away from the nest during incubation recesses (A) or when she is on the nest in the sleeping posture (C), while transparency indicates inactivity on the nest in (A) or any behaviour other than sleep in (C). The x-axis displays two consecutive days and these consecutive days are also shown from top to bottom on the y-axis. On the y-axis t = 0 is the day the first pictures were taken by the wildlife cameras. Population level graphs show the fraction of time, averaged over 24 hrs., spent on incubation recesses B) and in sleep posture D) in percentages (y-axis). The x-axis displays time over 24 hours, and the black line represents the mean, while in grey bootstrapped 95% confidence intervals are displayed.

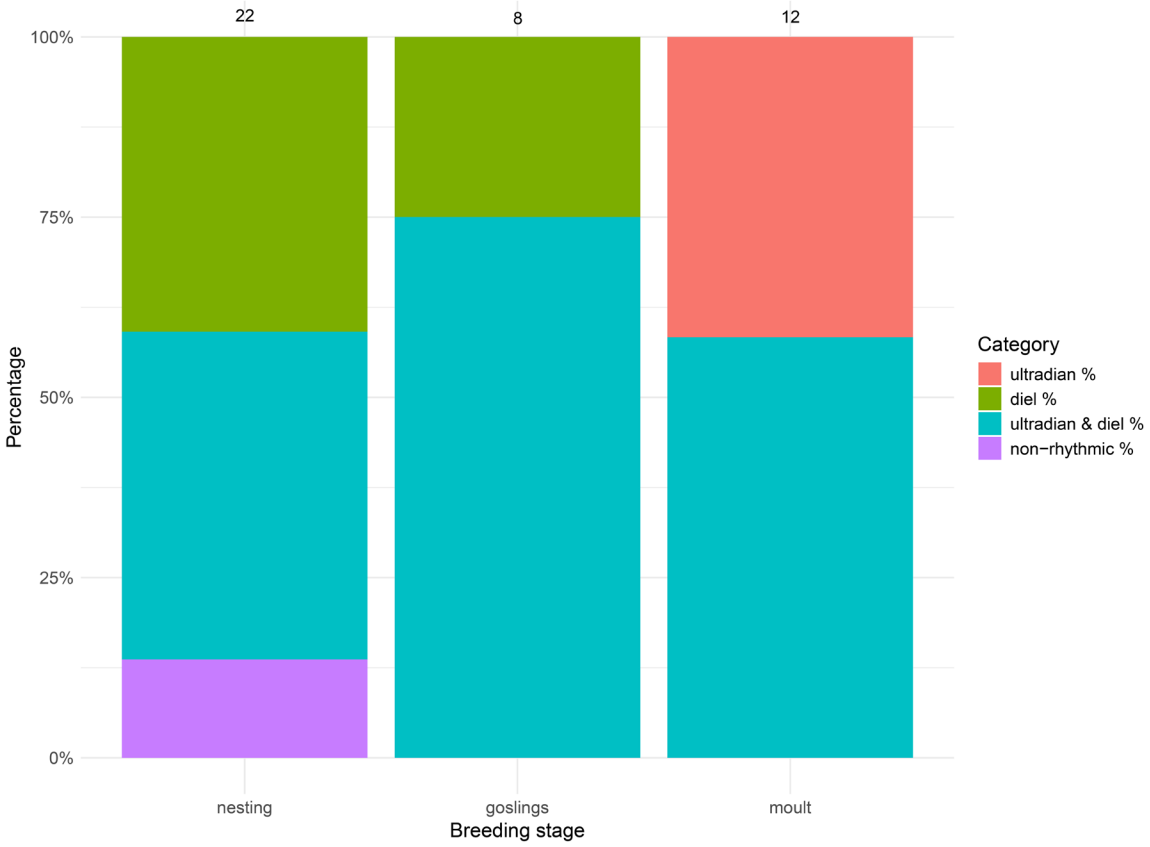

Figure 2: Percentages of 18 individual geese in total over the course of two years, which over the three breeding stages showed either ultradian or diel rhythmicity alone, a combination of ultradian and diel rhythmicity, or no rhythm. Numbers above the stacked bars indicate sample size per breeding stage.

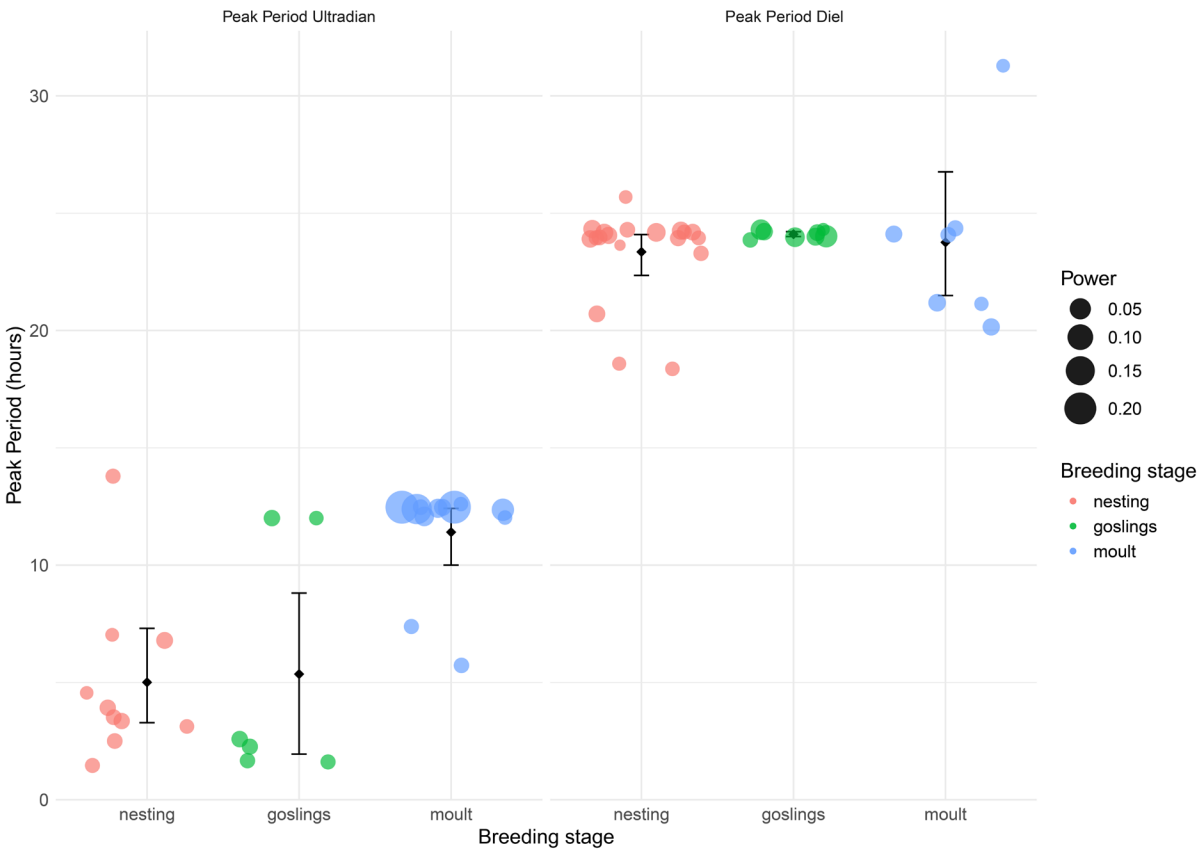

Figure 3: Diel and ultradian average peak periodicity during different breeding stages. The values of the peak period are for rhythmic geese only, i.e. a peak above the significance threshold at α = 0.05. Individual geese are shown by dots. The size of the dots represents the power of the peak period. The error bars are 95% bootstrap confidence intervals on the population mean.

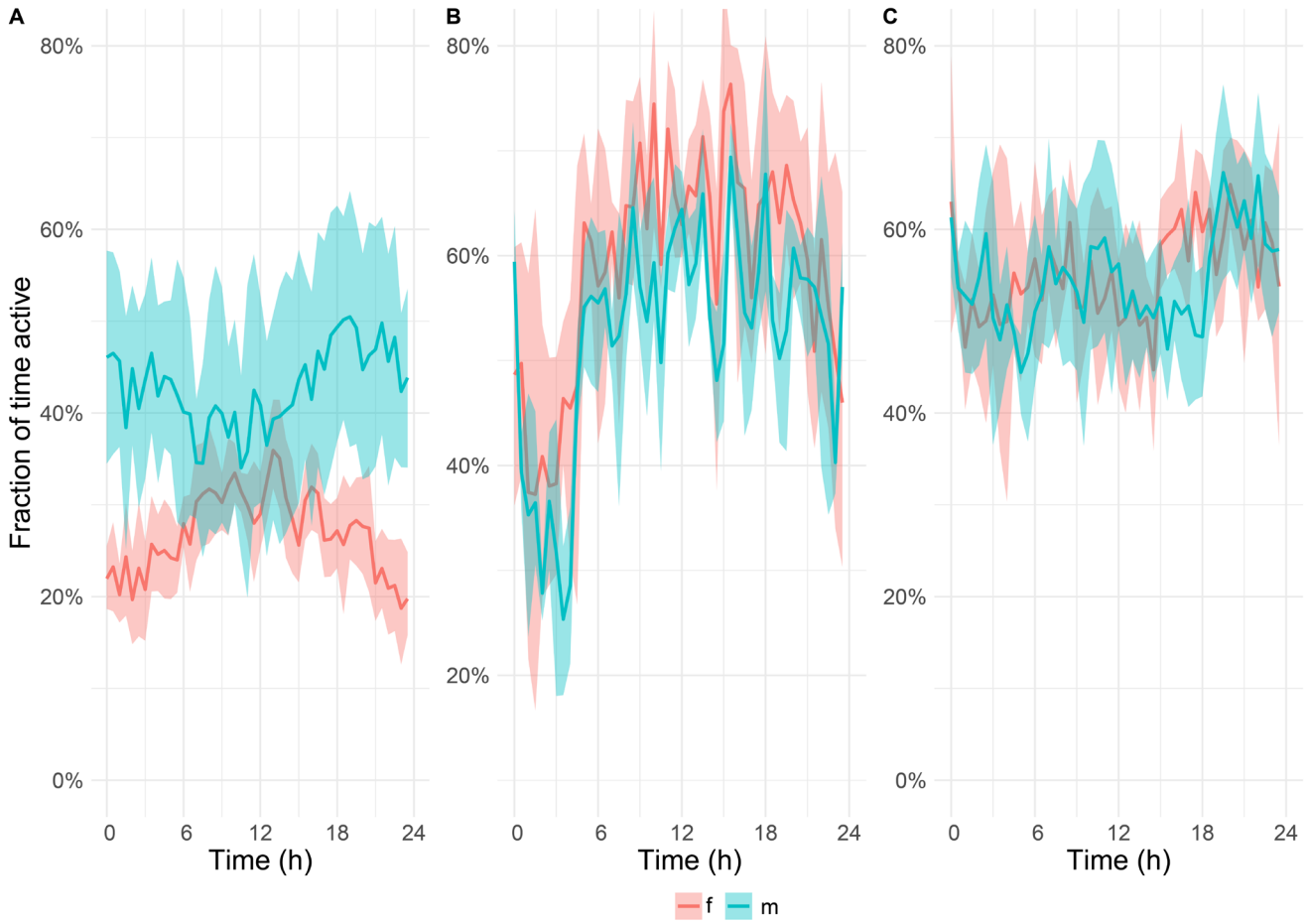

Figure 4: Population level graphs showing the fraction of time active, averaged over 24 hrs., during nesting (A), when geese had goslings (B), and during moult (C) in percentages (y-axis). Females (f) and males (m) are indicated in different colours. The x-axis displays time over 24 hours, and the solid lines represents the mean, while in transparent colour bootstrapped 95% confidence intervals are displayed.

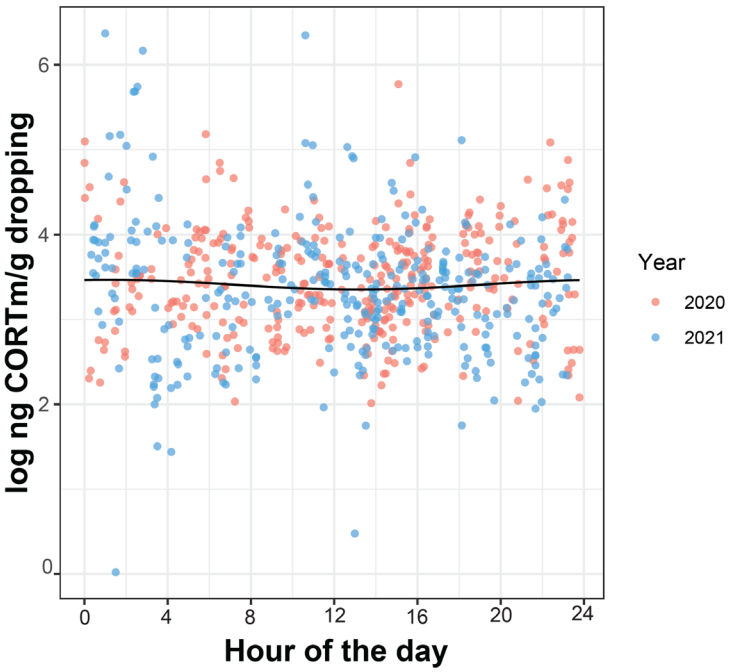

Figure 5: Daily rhythmicity in log-transformed corticosterone metabolite concentration measured in barnacle goose droppings. The solid line represents the predicted values from the model.