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

Margje E. de Jong * [1,3], Annabel J. Slettenhaar [2,3], Rienk W. Fokkema [4,5], Marion Leh [1], Mo A. Verhoeven [6,7], Larry Griffin [8], Eva Millesi [1], Børge Moe [9], Elisabeth Barnreiter [1], Maarten J.J.E. Loonen [3], Isabella B.R. Scheiber [1]

*corresponding author

(1) Dept. of Behavioral and Cognitive Biology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria

(2) Faculty of Biosciences and Aquaculture, Nord University, Kongens Gate 42, 7713 Steinkjer, Norway

(3) Arctic Centre, Aweg 30, 9718 CW Groningen, The Netherlands

(4) Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Nijenborgh 7, 9747 AG, Groningen, The Netherlands

(5) BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Wirdumerdijk 34, 8911 CE Leeuwarden, The Netherlands

(6) NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, The Netherlands

(7) Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands

(8) ECO-LG Ltd, Crooks House, Mabie, DG2 8EY, United Kingdom

(9) Norwegian Institute for Nature Research (NINA), PO Box 5685 Torgarden, 7485 Trondheim, Norway

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Abstract

Birds that migrate from temperate areas to the Arctic to breed lose their strongest *Zeitgeber* of circadian organization when they cross the Arctic circle in spring: the 24h light-dark cycle. Under continuous daylight, diverse 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 barnacle goose (*Branta leucopsis*), during its Arctic breeding season in Svalbard. We found that females showed a combination of both ultradian and diel rhythmicity in nest recesses and sleep during incubation. In both parents, these rhythms in activity continued also during the gosling rearing period. 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 maintain a diel rhythm, ultradian rhythmicity remains essential, allowing the geese to flexibly adjust their rhythms to environmental conditions.

Keywords

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

56 **1. Introduction**

57 Various biological processes occur rhythmically, restricted to specific times of the day or season [1,
58 2], and in many species are regulated by photoperiod – the environmental period of daylight – as a
59 *Zeitgeber* [3]. Upholding these rhythms in polar regions is challenging insofar as above the Arctic and
60 below the Antarctic circle (66°N and S) natural light is completely absent in winter but continuously
61 present during the summer [4]. Nevertheless, various Arctic species are able to retain endogenous and
62 behavioural rhythms [reviewed in 1, 5].

63 Arctic vertebrates show variation in rhythmicity in behavioural activity between species, between
64 individuals and within individuals. Arctic species are highly variable in their behavioural activity with
65 some species (i) being completely *arrhythmic,* (ii) showing *circadian or diel rhythmicity, i.e.*
66 displaying a recurring rhythm of approximately 24-hours even in the absence of light fluctuations, (iii)
67 showing *ultradian rhythmicity* of recurrent periods of foraging and resting bouts less than 24-hours, or
68 (iv) showing *free running rhythmicity, i.e.* not synchronized with environmental time cues [1, 5]. For
69 herbivore species, Bloch *et al*. suggested that ultradian activity patterns in polar regions are linked
70 with feeding behaviour and digestive processes [6]. Between individual differences exist, for example,
71 in migratory shorebirds displaying bi-parental care, where conspecific pairs may show different
72 incubation rhythms even when they breed in the same area [5, 7]. Furthermore, patterns may vary
73 seasonally within individuals, *e.g.* driven by annual changes of day length [5, 6]. For example, the
74 Svalbard rock ptarmigan (*Lagopus muta hyperborea*), the sole permanent resident bird on Svalbard,
75 exhibits ultradian activity patterns with periodic feeding during polar summer and winter days. In
76 contrast, during spring and fall its activity patterns are diurnal and feeding mainly occurs within
77 daylight hours [8]. The diversity in behavioural responses to continuous daylight underlines the
78 plasticity of the circadian system and indicates the relevance of the species' biology [5, 9].

79 Behavioural and physiological processes are regulated through the rhythmic excretion of
80 hormones by an endogenous network of one or several 'Master' clocks, which then coordinate and
81 synchronise more peripheral clocks [reviewed in 1, 2]. Crucial for tracking environmental cycles is
82 the neurohormone melatonin. Its diel secretion pattern, *i.e.* an extended peak at night and basal

secretion during the day, provides the paramount hormonal signal transducing day length for peripheral clocks [3]. Melatonin secretion drives lasting changes in the hypothalamic-pituitary adrenal axis (HPA), where low levels of melatonin culminate in the increased secretion of the adrenal glucocorticoids, *i.e.* cortisol in mammals and corticosterone (CORT) in birds [1, 10, 11]. Glucocorticoids are (i) involved in correlating peripheral clocks [12], (ii) best known as being the downstream effectors of one of the two major stress response systems [13], and (iii) interrelate with feeding, modulation of energy storage and mobilisation as well as activity [10]. They display robust diel rhythmicity in latitudes with year-round day-night cycles [14-16, but see 17]. In temperate zones, the diel rhythmic pattern of baseline CORT correlates with activity; low levels of CORT during inactive phases are followed by a rise just before activity begins and CORT remains high as long as birds are active [10]. Contrary, in polar species with 24 hours of continuous natural light during the summer, findings of a diel CORT rhythm are ambiguous. For example, common murres (*Uria aalge*) maintain a diel CORT rhythm in the polar summer [18]. In contrast, the link between activity, time of day and corticosterone is not evident in thick-billed murres (*U. lomvia*) [10]. Other species without a diel CORT rhythm are Adélie penguins (*Pygoscelis adeliae*) [4] and common eiders (*Somateria mollissima*) [19]. Arrhythmicity in CORT was attributed to the suppression of melatonin secretion when photoperiod as *Zeitgeber* is absent [5, 10, 19]. Also, the lack of a rhythm in CORT in common eiders was linked to CORT interfering with the need to constantly forage [5], while in thick-billed murres it was ascribed to a stable modulation of energy storage and mobilisation [10].

Many bird species, which show rapid migration to their Arctic breeding grounds, experience large changes in daylight conditions en route, before they arrive in the polar regions with 24-hours of natural light. Latitudinal migrants may benefit from longer photoperiods at higher latitudes as for diurnal animals daily activity and foraging time can be increased [20]. Nevertheless, such quick fluctuations in light conditions present a significant challenge for circadian physiology [21-23]. There is a surprising variation in the response of migrants to continuous daylight [e.g. 5, 7], despite the fact that changing to a different rhythm may potentially be costly [24]. To increase our understanding of the evolution of plasticity in circadian clocks in migratory birds, it is thus necessary to study rhythmicity in behaviour and physiology in relation to the ecology of the species [e.g. 6, 7, 9].

Here we aim to quantify behaviour- and CORT-based rhythmicity in the barnacle goose, a migratory herbivore, during its breeding season in the Arctic using a multifaceted approach. Earlier findings on rhythmicity in barnacle goose behaviour and physiology are somewhat equivocal. 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 [25-27]. Likewise, 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 in adult barnacle geese, using three different approaches; (i) activity and sleep during incubation, which were determined using photos from wildlife camera's placed in the vicinity of the nest, (ii) activity across the breeding season of females and males, which was assessed using data from accelerometers (ACC), and (iii) CORTm concentration, which was determined from individually assigned droppings. Contrary to mammalian herbivores, where digestive processes dictate ultradian activity patterns [29, 30], barnacle geese do not possess complex digestive systems. However, their summer food retention time is increased by interrupting feeding with longer loafing spells [29]. We expected that barnacle geese would feed around the clock [*sensu* 23], which has been suggested to be a possible adaptation of Arctic herbivores to optimally utilize the peak in high quality food during the short summer [31]. If ultradian rhythmicity in activity is important, then we expected to find a weak or absent diel rhythm in CORTm. In contrast, if barnacle geese rely on an evolutionary-based endogenous clock to schedule their biology or respond directly to external diel cues, then we predicted diel rhythmicity in activity and CORTm throughout the breeding season, similar to some other polar species [e.g. 18, 32, 33].

2. Materials and Methods

(a) Study site and species

We collected data during the summers of 2020 – 2022 in a barnacle goose population nesting on islets in Kongsfjorden, Svalbard. Geese from this population migrate annually from their wintering grounds in the United Kingdom to Svalbard, stopping along the Norwegian coast [29], and thereby experiencing a wide range of daylight conditions. 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 hatching on the two main breeding islands of the study area, Storholmen and Prins Heinrichøya from June to the beginning of July (see [34, 35] for details). 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 the researcher approached the nest [35]. To minimize disturbance, we got information on possible nests of geese with transmitters (see below) on other islands, *i.e.* 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 the 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]. In our analyses, we defined the flightless period to start at the first observation of loss of all flight feathers, and to end 25 days later (from now on called ‘moult’).

In 2020, we fitted 12 females and 12 males from 24 pairs 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 a ~ 6 m hand-held noose pole to catch the bird around its neck, or (2) by catching the geese by hand, which was mainly possible for aggressive males that came close. All remaining geese were caught during annually performed catches, during which flightless

moulting geese are driven into corrals [29]. The 24 individuals were chosen following a suite of criteria, including that it would be desirable if both pair partners were marked with unique colour rings already (for details of criteria see [40]). We determined the sex of the birds from cloacal inspection [35]. During the incubation periods in 2021 and 2022, we deployed additional transmitters on three birds (one female and two males) and four birds (three females and one male), respectively.

(b) Activity during incubation and across the breeding season

(i) Incubation patterns from wildlife camera photos

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

We analysed pictures (n = 110739) with Timelapse2 Image Analyser (version 2.2.4.3, [41]). We quantified whether the female was (i) sitting on the nest, (ii) in 'sleep posture', *i.e.* head resting on back with beak often tucked under a wing [42], (iii) standing right next to the nest or (iv) absent from the nest. For further analyses of nest recesses, we pooled behaviours (iii) and (iv) as *active* and behaviours (i) and (ii) as *inactive*. For the analyses of 'sleep', we contrasted being in the sleep posture with the other behaviours. Males sometimes nest sit [40], but here we focussed on females only. Instances, where males nest sat, while females were on incubation recesses, were classified as (iv) absent from nest.

In total, wildlife cameras supplied data from 2 hours to 20 days. We only used data which exceeded the recommended minimum duration of ten days for biological rhythm analyses [43, 44]. We could assess activity, *i.e.* incubation recesses, and sleep patterns, from photos taken by the wildlife cameras in 11 out of 15 females. The other four cases were discarded, because data were insufficient due to nest (n = 2) or camera failure (n = 2).

194 *(ii) Seasonal activity from transmitter accelerometer data*

195 We used ACC data collected by the transmitters during the summers of 2021 and 2022 (2021: females
196 n = 8, males n = 9; 2022: females n = 9, males n = 9; same individuals across 2021 and 2022: n = 12).
197 The solar-powered transmitters were set to record a GPS-fix every 15 min when battery voltage was
198 75-100%, every 30 min at 50-74%, every 60 min at 25-49% or every 240 min at voltages lower than
199 25%. Immediately after each GPS-fix, a 2-sec ACC burst was taken at a frequency of 20 Hz.
200 Gravitational acceleration was measured in unit g/1000 in the three spatial axes [45].

201 We used ACC data to identify activity and inactivity of individual geese during the breeding
202 season [46, 47]. For each goose, we checked the number of measurements per burst taken after each
203 GPS-fix to ensure a complete dataset. Then, we calculated the vectorial sum of dynamic body
204 acceleration (VeDBA) from the ACC data, a common proxy for energy expenditure [48]. For this, we
205 first calculated static acceleration, *i.e.* the average raw measured acceleration for each dimension (x,
206 y, z) within the bursts. Second, we subtracted the static acceleration from the raw data for each
207 dimension, thus getting dynamic acceleration. Last, we calculated the vectorial sum of dynamic body
208 acceleration of each burst by taking the square root of the summed dynamic accelerations of each
209 dimension [48]. Following [47], we created probability density histograms to identify peaks for
210 activity and inactivity and used the *mix* function in the R-package *mixdist* to decompose the
211 distribution into two gamma distribution components for active and inactive behaviour [49]. We
212 found the threshold between the active and inactive behaviour distributions by calculating the
213 intersection point between the two [see electronic supplementary material Figure S1, 46, 47].

214 In addition, we estimated the nesting period based on the method described by [45] using
215 VeDBA and GPS data. Nesting is defined as the entire period of egg laying, nest building, incubation,
216 and hatching. For females, we took daily median VeDBA < 1 for motionless days, as this
217 corresponded best with observed periods of nesting in the field (n = 14: nesting period or part of the
218 nesting period could be estimated, n = 3: nesting period could not be estimated due to transmitter
219 attachment during hatching or when the goose was likely not breeding). We estimated the potential
220 nest location by taking the median latitude and longitude of motionless fixes on days on which the

221 goose was mostly motionless. Nest site attendance was calculated as the distance of each GPS-fix of a
222 goose to its potential nesting location and then calculating the daily amount of time that the goose
223 spent within a radius 50 m of its potential nest site. The attendance threshold was the first day on
224 which the goose spent > 75% of time within 50 m of the nest and the period threshold was set at 3
225 days [45].

226 Most males, on the other hand, were never motionless during nesting (n = 14). Four males,
227 however, did show motionlessness, which could plausibly be used to establish the nesting period. For
228 nine additional males we established nesting based on field observations of the known nest location.
229 For six males, however, neither method worked and we could not establish nesting.

230 In total, we obtained both an observed nest location in the field and an estimated nest location
231 based on the transmitter data for 14 geese (males and females); the distance between the observed and
232 estimated nest location was 2.37 meters on average (SD = 0.98, range 0.85 – 3.67; we excluded an
233 outlier of 25.45 meters where the handheld GPS was likely turned on too late).

234 Later breeding stages, *i.e.* when geese had goslings and/or were moulting, were based on direct
235 observations (see above). For 13 geese we obtained data on the period with goslings, for 11 geese
236 when they were moulting and for three geese that had goslings while moulting ('goslings & moult'
237 period). Since these different breeding stages pose different demands on the geese [29], we tested for
238 rhythmicity within these three periods. Once again, we only used data, which exceeded the
239 recommended minimum duration of ten days for biological rhythm analyses. Therefore, we excluded
240 four nesting periods, five gosling periods, one gosling & moult period and one moult period, because
241 here data collection time was too short. We pooled the remaining two goslings & moult periods with
242 the moult period data to increase sample size.

243 **(c) Sample collection and corticosterone metabolite assay**

244 To investigate diel rhythmicity of CORTm excretion, we collected droppings of ringed geese in the
245 village of Ny-Ålesund from 1/7/2020 to 13/8/2020 (n = 349 droppings, 26 individuals; 14 females, 12
246 males) and 16/6/2021 to 31/7/2021 (n = 333 droppings, 52 individuals; 28 females, 24 males). For 17
247 individuals we collected samples in both years. We attempted to collect a minimum of three samples

248 [50] per 3-hour time intervals, *i.e.* from 0:00 – 2:59, 3:00 – 5:59, …, 21:00 – 23:59 and intended to
249 cover one complete 24-hour cycle every week for each individual. This was often not possible, as
250 pairs sometimes left the area and could not be located. Only unambiguously assigned samples were
251 collected and frozen at -20°C within 1 h (for methodology on how to collect droppings, see electronic
252 supplementary material). Droppings were shipped frozen to the Dept. of Behavioural and Cognitive
253 Biology, University of Vienna, Austria, for analyses.
254 Dropping samples for determining CORTm were quantified using an enzyme immunoassay
255 validated for barnacle geese [51] and applied successfully in previous studies [*e.g.* 28]. CORTm was
256 below the detection limit in three samples (total n = 679). Determined from homogenized pool
257 samples, intra- and inter-assay coefficients of variation (% CV) were 11.91% (< 15%) and 13.03% (<
258 25%), respectively.

259 **(d) Statistical analyses**

260

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

262 *(i) Rhythmicity in activity*

263 We plotted actograms to visualize overall activity patterns during incubation, as assessed from
264 wildlife camera data, and across the entire breeding season as determined from transmitter data
265 (*ggetho* package [52]). Actograms, which show rhythmicity or a lack thereof, were double-plotted to
266 facilitate inspection. We tested for periodicity in actograms using Lomb-Scargle periodogram (LSP)
267 analysis [*periodogram* function, *zeitgebr* package: 52, 53] during specific periods: *i.e*. the limited time
268 frame when cameras were placed during incubation until we spotted the first gosling on an image, and
269 the entire nesting period (defined as the total time of nest building, egg laying, incubation, and
270 hatching) as well as gosling rearing and moult for the transmitter data. The LSP analysis was suitable
271 to discover periodicity in our dataset as it can handle unequally sampled time-series with missing data
272 [53]. Periodicity, *i.e.* the regular recurrence of behaviour or an event over fixed, equal time intervals,
273 is a common but not universal trait of rhythmicity, which in itself emphasizes the repetitive pattern of

274 changes rather than precise timing [54]. For each dataset we ran two LSP analyses; one focussed on
275 ultradian rhythmicity with a period range between 1 and 18 hours and another focused on diel
276 rhythmicity with a period range between 18 and 36 hours [following 32, 44, 55]. Data were re-
277 sampled every 5 minutes in the case of data from nest cameras and every 15 minutes for data provided
278 by the transmitters. The oversampling rate was set at 100. We used the *find_peaks* function from the
279 *zeitgebr* package to extract significant peaks ($p < 0.05$). Time-series data can contain two separate
280 peaks, which may point to a true combination of ultradian and diel rhythmicity or it can be a data
281 artefact [56]. We followed the methods of [55] to distinguish between these two: if we found two
282 peaks in the normalized power for the same individual with an 18 h window we rejected the smaller
283 peak if it was less than one-third the height of the larger one.

284 We investigated possible differences in ultradian and diel peak periods between breeding stages
285 (nesting, goslings and moult) using linear mixed-effects models (*lme* from the package *nlme,*[57, 58])
286 with peak period in hours as the response variable and breeding stage (categorical) as a predictor
287 variable. In addition, we also considered the predictor variables sex (categorical: female, male), the
288 interaction between sex and breeding stage, and year (categorical). We accounted for repeated
289 measures by adding ID as a random effect. We used automated model selection using the function
290 *dredge* (package *MuMIn*) and AICc [59]. We give the 95% confidence set of models in the electronic
291 supplementary material [60] and information including 85% confidence intervals for the full model in
292 the text [61]. The 85% interval is consistent with how variables are selected using AIC. When present
293 in the top model, we computed estimated marginal means for specific factors and comparisons among
294 levels [package *emmeans*, 62].

295 *(ii) Diel patterns of immune-reactive corticosterone metabolites*

296 To investigate the association between predictor variables and CORTm concentration over the day,
297 we fitted linear fixed-effects models (*lme*). We log-transformed CORTm concentration to adhere to
298 model assumptions. The predictor variables in all models include time of day (continuous), year
299 (categorical), day of the year (continuous) and sex (categorical). As time of day is a circular variable,
300 we changed it into two linear variables by first transforming hour of day to radians and then

301 calculating the sine and cosine of those radians. We included sine and cosine as continuous predictor
302 variables in our models [18, 63]. To account for repeated measures of the same individuals, we added
303 individual identity as random factor in all models. A more complex random slope model could not be
304 explored, because this fitted mixed model was singular. As above, we used model selection using the
305 function *dredge* (package *MuMIn*) and AICc and give the same model information.
306

307 ## 3. Results

308 ### (a) Rhythmicity in activity

309 #### *(i) Rhythmicity during incubation*

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, in nine females we found both
316 ultradian and diel rhythmicity when resting in a sleep posture (Figure 1C, for actograms of all females
317 see 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 #### *(ii) Seasonal rhythmicity in activity*

322 We detected rhythmicity in all geese over the course of the entire breeding season (for examples of
323 actograms of two individuals see electronic supplementary material Figure S6). Except for three
324 females, which showed no rhythmicity in activity patterns during nesting in 2022, most geese showed
325 diel rhythmicity or a combination of ultradian and diel rhythmicity during nesting and when they had
326 goslings (Figure 2 left and centre panel). Furthermore, we also detected either ultradian rhythmicity
327 only or a combination of ultradian and diel rhythmicity during moult (Figure 2 right panel). We found

evidence that breeding stage correlated with ultradian peak period, as this variable was present in all models within the 95% confidence set (Table 1A, electronic supplementary material Table S3). The top model included breeding stage only (Table 1A) and post-hoc testing revealed that the ultradian peak period during moult was significantly higher than when geese nested or had goslings (Figure 3, goslings – moult; estimate = -6.05, SE = 1.75, p = 0.015, goslings – nesting; estimate = 0.35, SE = 1.80, p = 0.9794, moult – nesting; estimate = 6.40, SE = 1.49, p = 0.004). There was no strong indication that breeding stage influenced diel peak period, with the top model being the null model (Table 1B, Figure 3, see also electronic supplementary material Table S4). The fraction of time when the geese were active, varied between males and females during nesting, with females being more active around noon, while males were less active then (Figure 4A). When geese had goslings or were moulting, females and males did not differ in the fraction of time they were active (Figure 4B & C), but there was a sharp decrease in activity after midnight until early morning. This pattern was not present during moult.

(b) Diel patterns of immune-reactive corticosterone metabolites (CORTm)

Our results revealed that CORTm concentration was marginally influenced by time of day (Table 2), with both cosine and sine of time of day being present in the top model as well as in many models within the 95% confidence set (electronic supplementary material Table S5). CORTm concentration increased during conventional night time and decreased during day time hours (Figure 5). CORTm 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).

4. Discussion

Svalbard barnacle geese maintain rhythmicity in behaviour and physiology 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. Most females and males also showed a combination of ultradian and diel rhythmicity or diel rhythmicity only in activity during their entire nesting period or when they had goslings. During moult, geese exhibited either ultradian rhythmicity alone or a combination of ultradian and diel rhythmicity in their activity, possibly indicating a response to tidal rhythms (see below). 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. Below we discuss our findings in more detail.

(a) Ultradian rhythmicity in goose activity behaviour

Our results indicate the significance of ultradian rhythmicity, *i.e.* periods of less than 24 hours, in activity behaviour over the breeding season. 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 [27], 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. 44, 55, 64, 65]. Such an activity pattern could be endogenously generated by ultradian oscillators [65] or controlled by the interplay of feeding and digestion [6, 66].

(b) Diel rhythmicity in goose activity behaviour

Many geese also showed diel activity patterns in behaviour, *i.e.* periods of around 24 hours, throughout the breeding season. The presence of a diel rhythm does not inherently imply, however, that circadian systems are functional and/or entrained as the geese could be reacting directly to external cues, also known as “masking” [1, 67]. For example, during nesting, female geese could

respond adaptively to temperature differences between conventional day and night, with slightly higher temperatures during the day despite 24h daylight. This might limit egg cooling rates during incubation recesses, as shown in snow geese [*Anser caerulescens*, 68]. Males do not incubate, although they sometimes sit on the nest [40], but often stand guard close by the nest when the female is on incubation recesses [27]. Nests, however, are more vulnerable to predation if the female is on recess [69] with the most significant egg predators, glaucous gulls (*Larus hyperboreus*) and Arctic skuas (*Stercorarius parasiticus*), being more active during conventional daytime [25]. This conflicts with females being on recesses then. Arctic foxes (*Aleopex lagopus*), on the other hand, are usually more active at night [25, pers. obs.]. For more than a decade, however, no foxes have been observed on those islands, where nests were monitored (pers. obs.). By contrast, foxes have been present in the gosling rearing areas during the study years. Here, males and females usually rested close to water bodies, into which they could escape from the fox [38, pers. obs.]. Although barnacle geese may not be able to protect their nests against foxes even if both parents are present [34, 70], fox predation was suggested to be the selective force of the observed diel rhythmicity during incubation [25] as a 'ghost of competition past'. If the day-active behaviour of female geese during nesting is shaped by an expected daily rhythm in fox predation risk, it suggests the activity pattern is regulated by an endogenous, innate circadian mechanism [71]. It is feasible that a goose's circadian clock continues to function by employing alternative potential *Zeitgeber*s, such as diurnal changes in light intensity, polarization patterns, solar azimuth, UV radiation, changes in the spectral composition of light or slight changes in ambient temperature, which exist under polar summer conditions [72].

(c) Ultradian and diel rhythmicity in sleep

Studies on sleep patterns under natural conditions are rare due to challenges in measuring sleep in wild free-moving animals [73]. During incubation, we scored sleep posture, which has been associated with rapid eye movement (REM) sleep and non-REM (NREM) sleep in domesticated geese [42]. We therefore assume that our behavioural scoring of sleep was valid overall, although misclassifications may have occurred if individuals fell asleep while sitting with their beaks pointing forwards or were awake in the typical sleep posture. In addition, various bird species, such as mallards

410 (*Anas platyrhynchos*) for example, perform unihemispheric sleep [74], which we could not measure
411 here. The diel sleep pattern contrasts distinctly with the diel pattern observed in nest recesses (Figure
412 1), with females sleeping more during the conventional night. In addition, we detected ultradian
413 rhythmicity, with a mean peak period of ~ 8 h. Awakening bouts could serve as a periodic screening
414 of the environment for danger [74, 75]. Captive barnacle geese kept under a natural day - night cycle
415 also showed scattered sleep over the course of the day during summer [76], and the authors proposed
416 that barnacle geese might have an attenuated circadian organization and may profit from becoming
417 arrhythmic during the polar summer. However, we found no strong evidence for arrhythmia.

418 **(d) Tidal rhythm in goose activity during wing moult**

419 During wing moult, barnacle geese are most vulnerable to fox predation [69]. At times, when goslings
420 are still present, parents are forced to forage in areas with high quality food even during moult,
421 thereby risking higher predation [38]. When goslings are preyed upon, adults can retreat to areas with
422 lower-quality food but higher safety, such as tundra lake shores with mossy vegetation [38]. Over the
423 past years, we noticed moulting geese without young to increasingly utilize the intertidal area to rest
424 and/or forage on algae (pers. obs.). The ~ 12 h ultradian rhythmicity patterns of geese during moult
425 reflect the falling and rising tides (Figure 3, electronic supplementary material Figure S6A, [77]). The
426 tides pose a constraint on an all-day-activity [78, 79], but the nearby sea provides safety from foxes.
427 Additionally, the enhanced digestion during moult may help geese process and extract nutrients from
428 this otherwise difficult-to-digest food [30, 80]. Although barnacle geese were shown to avoid salt-
429 marsh vegetation in spring when it was experimentally sprayed with seawater, because they
430 presumably are less capable of physiologically coping with very high salt loads in their environment
431 [81], moulting geese foraged on algae in our study, possibly benefitting from fresh river water nearby.
432 Moult in geese is energetically costly, because they moult wing coverts, some body feathers and flight
433 feathers simultaneously. To compensate, geese become less active overall (Figure 4C, [39]). In
434 contrast, geese, which still lead young, seem to retain their activity rhythm also throughout moult.
435 This should be investigated in the future, because here sample sizes of geese with goslings were too
436 small to confirm this finding.

437 **(e) Weak diel rhythmicity in corticosterone metabolites (CORTm)**

438 Besides rhythmicity in activity, geese also maintained an, albeit weak, rhythmic pattern of excreted
439 CORTm (Figure 5), similar to what we found in human-raised barnacle goslings over 24 hours [28].
440 Glucocorticoids are integral in providing physiological signals to regulate biological rhythms in sync
441 with daily environmental cycles linking with activity and feeding [11, 12]. During the gosling period,
442 when we collected the majority of samples for CORTm measurements, our finding contradicts this
443 general assumption, because values dropped from conventional midnight to being lowest around
444 midday, when geese are most active. As discussed in an earlier study [28] as well as above, increased
445 fox activity at night, during the period when the goose families preferentially rest, could have affected
446 the CORTm rhythm. In sum, whether the attenuated rhythm in CORTm is sufficient to regulate
447 activity patterns and other functions during the polar summer or whether it plays only a minor role in
448 endogenous timekeeping [18] needs to be investigated in the future.

449 **(f) Suitability of the methods used**

450 Our use of a multifaceted approach, combining behavioural observations via wildlife cameras and
451 accelerometers with corticosterone measurements, allowed for a comprehensive understanding of
452 rhythmicity in barnacle geese during their Arctic breeding season in 24h daylight. We found
453 accelerometers to be a suitable alternative for investigating activity, where time consuming direct
454 behavioural observations are difficult. They are a valid substitute also for pictures obtained from
455 wildlife cameras, where a multiplicity of photos need to be analysed in detail afterwards. For
456 example, we found that the peak period in activity of five females during incubation, identified from
457 both wildlife cameras and accelerometers corresponded very well. Except for one female, where we
458 found diel rhythmicity retrieved from the ACC data which was not detected in data from the wildlife
459 cameras, the ACC-based activity patterns gave reliable results in the other four individuals, despite
460 the slightly longer 15 min intervals of ACC measurements relative to the 5 min intervals of
461 subsequent photos (ultradian: camera data; mean = 3.5 h, SD = 1.7, ACC data; mean = 3.8 h, SD =
462 1.7. diel: camera data; mean = 23.8 h, SD = 0.7, ACC data; mean = 24.2 h, SD = 0.1). This indicates
463 that ACC-based data described activity very reliably. This is supported by another study in captive

barnacle geese, which investigated sleep – wake rhythms. Here, activity measurements from ACC data correlated well with patterns retrieved from electroencephalograms (EEG) [76]. Contrary to our study, where ACCs were mounted in neck collars, these ACCs were head-mounted. They took high-frequency measurements at a high sampling rate of 100 Hz, and could, thus, record even small head movements. In our study data were less fine-tuned, because they were collected at a lower rate, *i.e.* every 15 min during 2-sec bursts of 20 HZ. Therefore, we cannot provide the same inferences at present.

(g) Conclusion

To summarize, over the course of their Arctic breeding season, barnacle geese show some degree of plasticity in their daily rhythms. Such intra-individual shifts in rhythms between sexes and breeding 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' or goslings' activity. The investigation of individual plasticity and consistency in behavioural and hormonal rhythmicity, and their relationship with fitness, are novel avenues for future work.

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).

Data accessibility.

Data and code used to conduct the analyses will be openly available in the Dryad data repository when the manuscript has been accepted for publication. Supplementary material will be available online.

Declaration of AI use.

As most authors are non-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.

Authors' contributions.

M.E.d.J.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing; A.J.S.: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing; R.W.F.: Investigation, Methodology, Validation, Writing – review & editing; M.L.: Investigation, Validation; M.A.V.: Investigation, Writing – review & editing; L.G.: Methodology, Resources, Writing – review & editing; E.M.: Resources, Writing – review & editing; B.M.: Funding acquisition, Writing – review & editing; E.B.: Investigation, Validation, Supervision; M.J.J.E.L: Investigation, Resources, Supervision; I.B.R.S.: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.
All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interests.

We declare we have no competing interests.

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Tables

Table 1: Intercept and coefficient estimates from the full models investigating differences in (A) ultradian peak period in hours and (B) diel peak period in hours with corresponding standard errors (SE), 85% Confidence intervals (lower, upper), and if the variable was selected in the top AIC model. For (A) the random intercept for individual ID had a standard deviation of 0.0001 and the residual standard deviation was 2.96. For (B) the random intercept for individual ID had a standard deviation of 0.87 and the residual standard deviation was 1.76.

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

Table 2: Intercept and coefficient estimates from the full model investigating rhythmicity in log-transformed corticosterone metabolite concentration with corresponding 85% CIs, and if the variable was selected in the top AIC model. The random intercept for individual ID had a standard deviation of 0.23 and the residual standard deviation was 0.67.

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

Figures

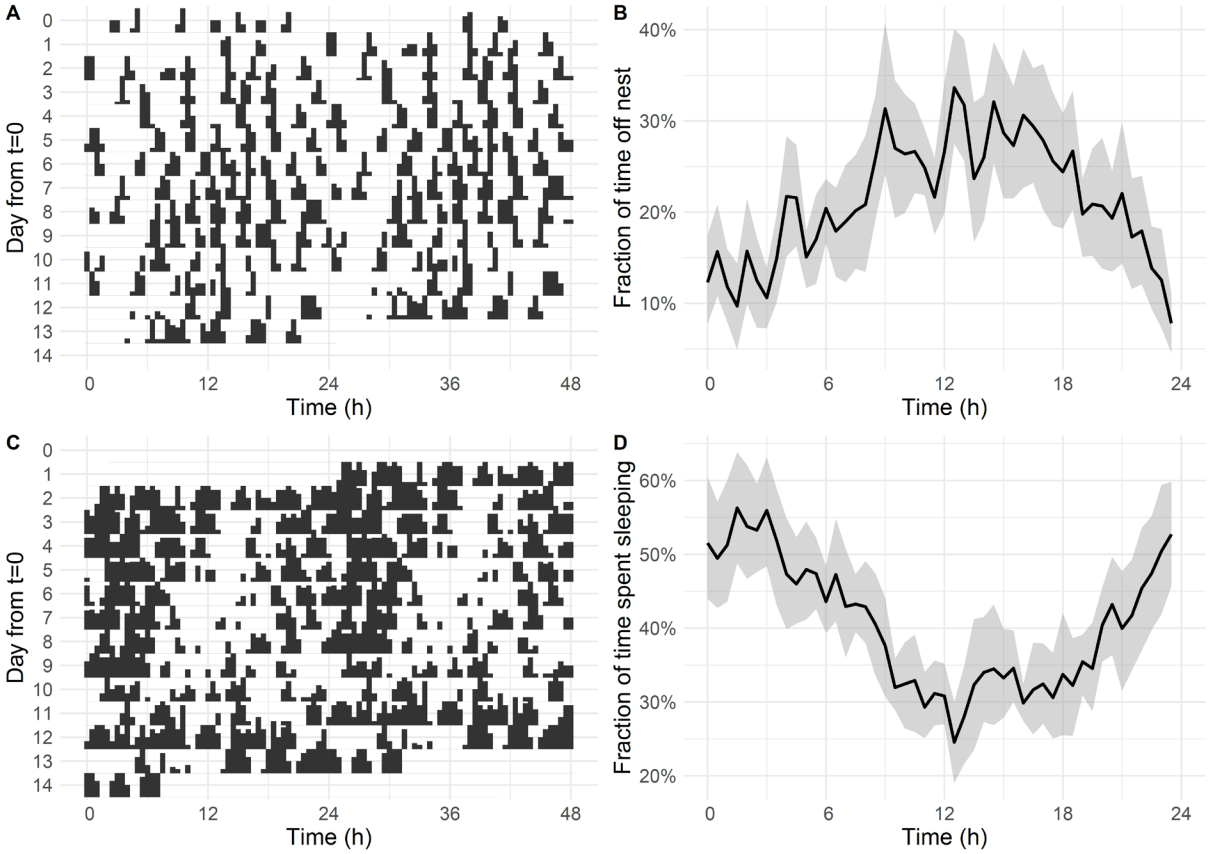

Figure 1: Rhythmicity of females during incubation recesses [panels (A) and (B)] and 'sleep' [panels (C) and (D)] based on wildlife camera pictures. Double plotted actograms of female ID CA41113 as an example show in black when she is away from the nest during incubation recesses (A) or when she is on 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 height of the bars indicates how often the specific behaviours are observed during that time. 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 (N = 11) graphs show the fraction of time, averaged over 24 hours, 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.

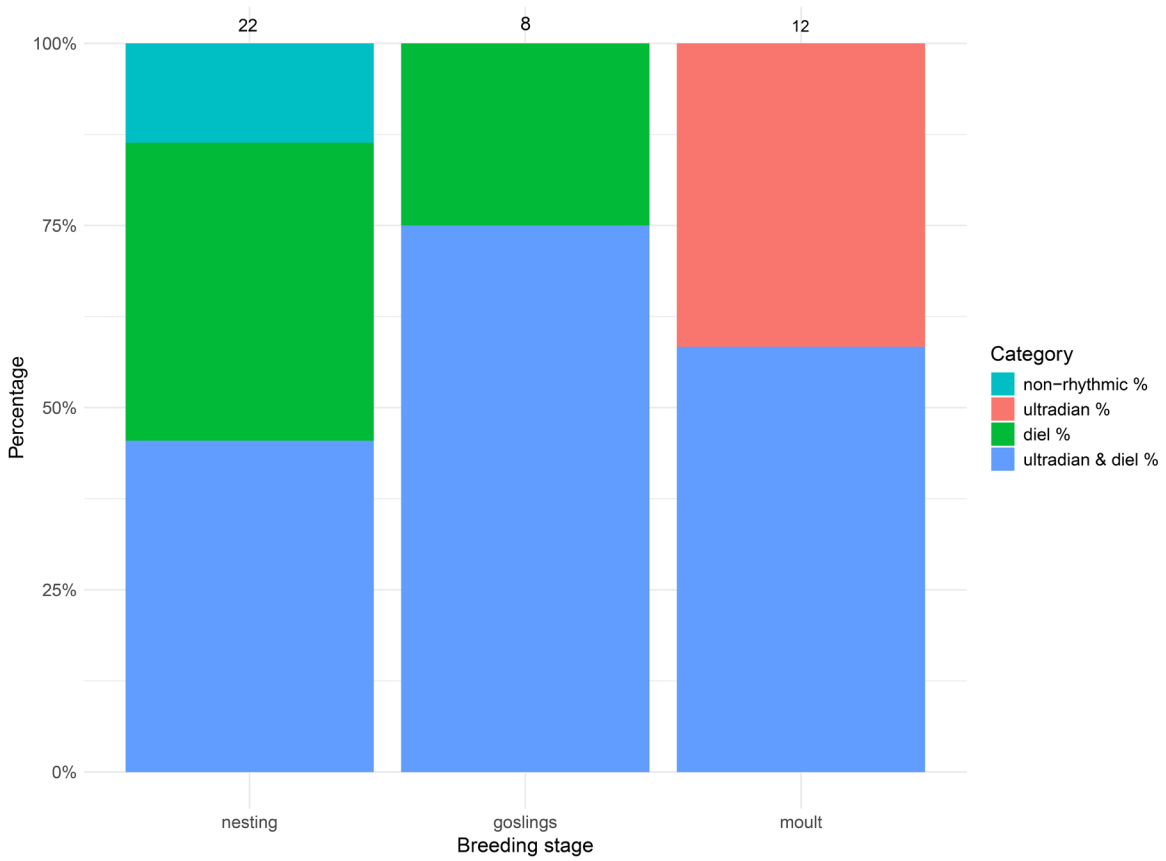

Figure 2: Percentages of rhythmicity types based on transmitter accelerometer data for 18 individual geese over the course of two summer seasons. Over the three breeding stages either ultradian or diel rhythmicity alone, a combination of ultradian and diel rhythmicity, or no rhythm were observed. Numbers above the stacked bars indicate sample size per breeding stage.

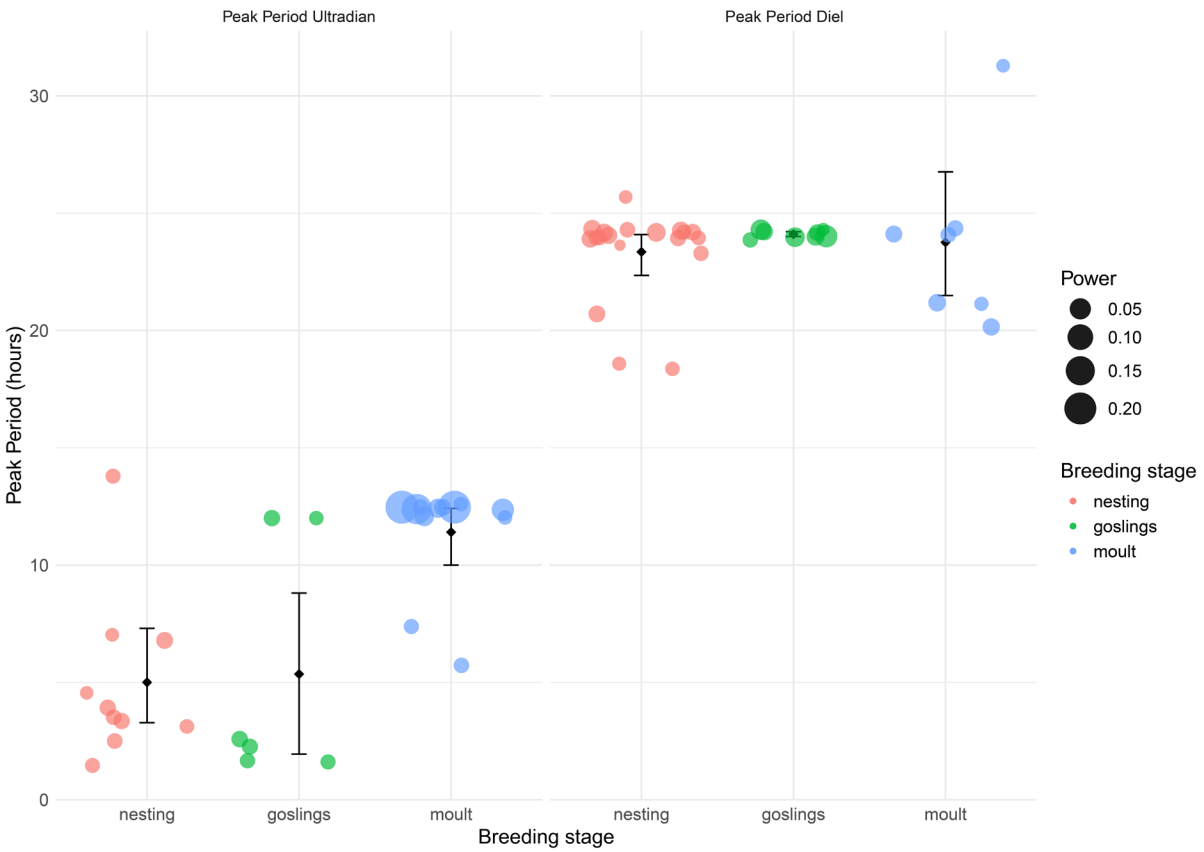

Figure 3: Diel and ultradian average peak periodicity during different breeding stages based on transmitter accelerometer data. The values of the peak period are for rhythmic geese only, i.e. a peak above the significance threshold at α = 0.05. Individual geese are shown as dots. The size of the dots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

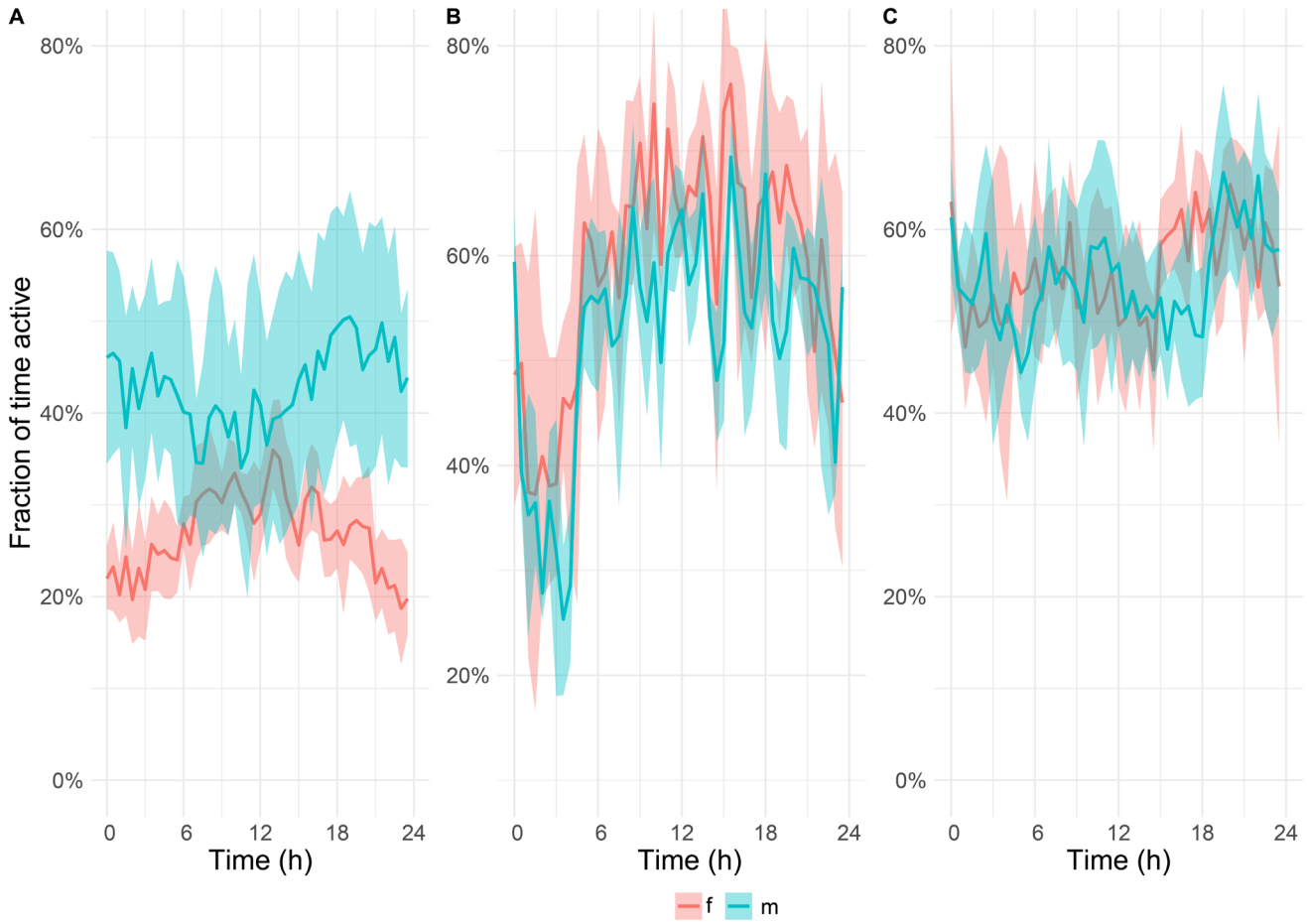

Figure 4: Population level graphs, based on transmitter accelerometer data, showing the fraction of time active, averaged over 24 hrs., during nesting (A), when geese had goslings (B), and during moult (C) in percentages (y-axis). Females (f) and males (m) are indicated in different colours. The x-axis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

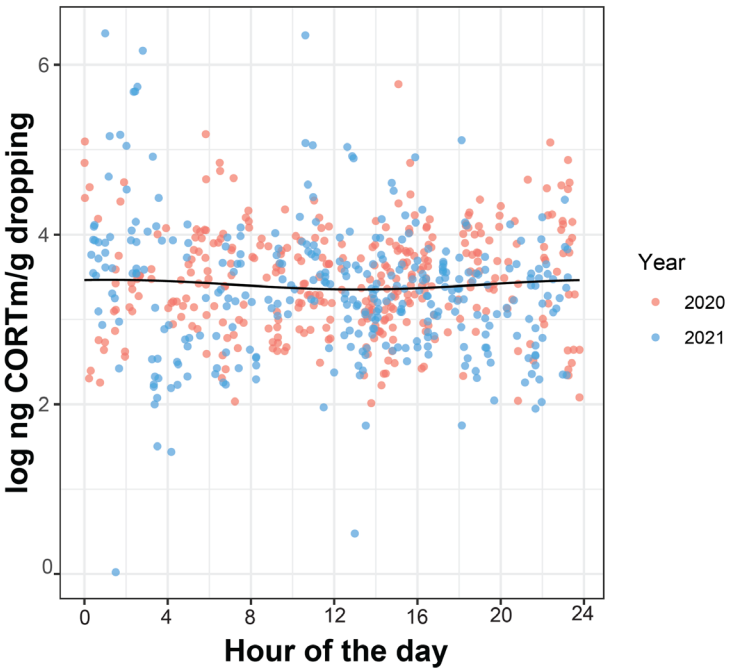

Figure 5: Daily rhythmicity in log-transformed corticosterone metabolite (CORTm) concentration measured in barnacle goose droppings in two years. The dots represent individual measurements and the solid line represents the predicted values from the model. 2020: n = 349 droppings, 26 individuals. 2021: n = 333 droppings, 52 individuals.