Chronotypes of the Great tit (*Parus major*) relative to heavy rainfall

Pradyut Rao, University of Groningen

Abstract

Species of all phyla have endogenous biological rhythms synchronized to external zeitgebers. The relationship between the two is called the phase of entrainment and when individuals differ in this trait, they are said to be different chronotypes. Chronotypes have been heavily investigated in humans and more recently, in other vertebrates and invertebrates mainly under laboratory conditions. In this paper we first investigate the occurrence of chronotypes in a free-living population of great tits (*Parus major*). Chronotypes were assessed using incubation temperature profiles and then compared on the differences in timing for the onset of activity, offset of activity and total daily activity period. Considering this year (2021) was an exceptionally bad year for the birds who were faced with frequent storms, we also investigate the difference in the aforementioned timings for the chronotypes as a result of heavy rainfall. We also look at its effect on fitness, described as the number of fledglings produced, of the chronotypes. We find that the birds show distinct early, intermediate and late chronotypes with the stratification being more conserved for onset than offset. Heavy rainfall led to all three chronotypes having an earlier onset on the day immediately after the rain and an earlier offset on the day of the rain. There was no significant difference between the chronotypes in fitness. We conclude that wild birds also show distinct chronotypes, with onset time providing a more robust estimate for chronotype providing incentive for studies in normal years on differences in other fitness estimates as well as studies on wild species of other phyla.

Introduction

Daily biological cycles are found in a wide range of species spanning all phyla and are a product of endogenous circadian rhythms. These rhythms are synchronized within the body using external cues called zeitgebers (light, temperature, humidity etc.) mainly produced through the alteration of light and darkness as a consequence of Earth’s rotation. An active process called entrainment works within an individual to help synchronize the biological clock with the zeitgebers forming an intimate temporal relationship. This association between the endogenous and exogenous factors is called the phase of entrainment and when individuals differ in this attribute, they are said to be of different chronotypes (Roenneberg et al 2003, 2007).

Chronotypes in humans have been extensively studied, mainly assessed using easy to answer questionnaires which were either subjective to the individual or relative to other individuals. All questionnaires evaluated “morningness” and “eveningness” of an individual. Identified morning types (MT) were found to advance their bedtimes and have a preference for early hours while evening types (ET) usually delay bedtimes and prefer evening hours. They have also been found to differ in their daily body temperature rhythms with peaks occurring at different times of day. (Horne et al 1980; Labyak et al 1997; Smith et al 2002; Roenneberg et al 2007). More recently a study by Facer-Childs et al. (2018) investigated performance differences between early and late chronotypes on several cognitive (psychomotor vigilance, daytime sleepiness) and physical (executive function, isometric grip strength) parameters. They found that late chronotypes were significantly compromised in all areas in the morning as compared to early chronotypes. These studies, including several others, have led people to believe that chronotypes in humans is an important facet to consider in various social fields such as sports, academics and corporate work (Smith et al 2002).

Considering how conserved the endogenous circadian rhythm is in species of all phyla and the subsequently evident chronological split in timing in humans, the study of chronotypes was only expected to have shifted into other less explored reaches of the animal kingdom. Chronotypes have been evaluated, with its causes and consequences studied in several vertebrate species (Common degu, *Octodon degus,* Labyak et al, 1997; Blue tits, *Cyanistes caeruleus,* Steinmeyer et al 2010; Great tits, *Parus major*, Helm and Visser 2010, Lehman et al 2012; Mice, *Mus musculus*, Wicht et al 2014; zebra fish, *Danio rerio,* Amin et al 2016; pine siskins, *Spinus pinus*, Rittenhouse et al 2019). Genetic underpinnings of chronotypes have also been investigated in invertebrates such as fruit flies (*Drosophila melanogaster*, Pegoraro et al 2015, Nikhil et al 2016).

However, all the aforementioned studies are cut from the same cloth in that they were all carried out in controlled laboratory settings. Additionally, most chronotyping is species-specific, such as the use of eclosion time in Fruit flies (Nikhil et al 2016), phase angle of entrainment in the Common degu (Labyak et al 1997) and activity onset in nocturnal and diurnal birds (Rittenhouse et al 2019; Lehman et al 2012). In this study we first investigate the presence of chronotypes in a free-living population of Great tits on Vlieland, an island in the Wadden sea. We predict, similar to Lehman et al (2012), that wild great tits will also exhibit different chronotypes and we test this using a method with incubation temperature profiles, designed exclusively for this field study. This year, 2021, was an exceptionally bad year for the birds on the island who faced regular storms (rain, strong winds and low temperatures) during the breeding period. This led to a delayed start to the breeding season, higher rates of nest desertion, low availability of food and high chick mortality rates. In the face of these adverse conditions the different chronotypes may be affected differentially owing to differences in daily timing. Early chronotypes may be able to offset delays in mating and feeding activities due to the storm by starting the day earlier. To investigate these possible differences, we also tested the effect of the storm (specifically heavy rainfall) on the daily timings and fitness (using total number of fledglings produced as a proxy for fitness) of pre-identified chronotypes.

Methods

Data collection

The project was undertaken on Vlieland (Atema et al, 2016), a west friesian island in the Wadden sea (between 53°17'45.1" N and 5°03'3.6" E) consisting of mixed forests with deciduous and pine trees. All nests were monitored in accordance with the protocols for the long-term monitoring project on the island and permission for animal experimentation was given to Marcel Visser, NIOO. During weekly checks, we scored nest building looking for any signs of fresh nesting materials (typically, green moss) in boxes that should have been emptied during initial pre-breeding checks as well as any laid eggs. Laying date was back calculated from the number of eggs in the nest during the check, as great tits lay 1 egg per day. Nests with at least 3 eggs on the day of checking had iButtons (Thermochron, DS1922L-F5 by Maxim Integrated Products) placed to record nest temperature fluctuations to assess incubation activity. The iButtons have a range of -40 to +85°C and can hold a total 4096 16-bit recordings (i.e. to the nearest 0.0625 °C). They were pre-programmed to take readings at equal intervals of 3 minutes (180 seconds) and were wrapped in thin silk sock, tightened with a malleable wire and carefully inserted into the nest among the eggs. Environmental temperature was recorded using HOBO loggers placed in 4 distinct locations around the island which measured temperature and light intensity.

The incubation period of the Great tit varies between individuals within a population, largely dictated by the environment. The average incubation period is anywhere between 12-14 days after the last egg has been laid (Alvarez and Barba, 2014). Great tit females only partially incubate during the day and slowly spend more time incubating on the nests, closer to hatching. Hatch date was accordingly calculated for all of our nests by keeping incubation day 14 as the expected hatch day and carrying out hatch checks on days 12, 14 and 16. These visits serve to check for hatches and obtain an age range for the nest using a visual pictorial aid to identify physical cues for chick age. Once the chicks were anywhere between 8-14 days old, the parents were caught using a spring-loaded trap and processed for age, sex, length of 3rd primary feather and length of tarsus. The chicks were ringed with aluminium rings and unringed adults were ringed with colour and aluminium rings. At chick day 15, all chicks were caught and processed as was done with the adults. The next (weekly) check after chick day 15 measurements served as final fledge check and fledged nests were cleaned.

Dataset formation and chronotype assessment

The final dataset for assessing chronotype and running statistical analyses was formed using the large pool of collected iButton data consisting of temperature fluctuation profiles of every incubation day of a nestbox. From these profiles we extracted the morning onset of a bird's active day which is the first off-bout from the nest in the day as well as the offset of the bird which is the last off-bout when the bird retires for the night. We also extracted the median of activity, which was calculated as the time when 50% of total activity (i.e.off-nest events) had occurred during the activity period of the bird (Wicht et al, 2013). Chronotype was then assessed by ranking onset of incubation and median of activity, of each nestbox per day, effectively giving us the chronotype of the nestbox of interest relative to other conspecifics. To enable ranking, we focused on nestboxes with iButton data from the 17th of April to the 30th of May (a total of 43 days). Nestboxes were individually selected one at a time and run through the R script consisting of a modified version of the IncR package developed by Pablo Capilla - Lasheras (2018) to analyse incubation behaviour. Using an input of parameter values, IncR provides an incubation profile of temperature fluctuations showing when the female leaves the nest (off-bouts) and is back on the nest (on-bouts). It does so by calculating the difference between the nest temperature (in the nest cup) and the environmental temperature, at any point in time within a specified time frame. In our setup, we set the *lower.time* at 20 (8 pm) and *upper.time* at 5 (5 am) which is the time window during which incubation is assumed to always take place, *sensitivity* at 0.05 (used in calculations only if environmental temperature and nest temperature are almost similar), the *temp.diff.threshold* at 5 and *maxNightVariation* at 5 which controls for the maximum temperature variation within the time window. The output consisted of all off and on-bouts of the female on the eggs and percentage time spent on the nest for each nestbox under consideration.

From this the first off-bout and last on-bout on a day, and median of activity were extracted as items of particular interest. Here we use onset of diurnal incubation as our proxy for the onset of incubation. This was calculated in IncR using 'IncRatt' which uses all on and off incubation bouts in a 24-hour period to calculate the percentage of time spent on the nest by the bird. We identified onset of diurnal incubation as the first date when the female had spent at least 60% of time on the nest and incubation profile data for all days post this were plotted till hatch date per nestbox. From these plots, all days with bad data where incR did not manage to accurately read onset, offset and all on and off bouts, were individually identified and physically filtered to control the quality of data and at the same time, making sure that the nestbox under inspection had at least 5 days of good data to ensure good statistical power. This process was then repeated for the next nestbox, ultimately compiling a large dataframe which had 68 nestboxes and a total of 1189 data points.

As briefly mentioned earlier, to assign a chronotype the nestboxes were first grouped by day and assigned a rank per day for both onset and median of activity. To ensure good power, days that had data for less than 7 nestboxes were discarded, with the final list spanning 27 days of the breeding period. Each nestbox thus had one rank per day of incubation for onset and median of activity, respectively. From this, the mean for the daily ranks of onset and median of activities for each nestbox was calculated leaving us with a list of unique nestboxes with one mean onset rank and one mean median of activity rank each. Finally, the mean of these two mean ranks gave us the relative chronotype rank of each nestbox from earliest to latest. The chronotype ranks were a continuous scale starting at 2.9 and going upto 20.75.

Rain day data

Rain days were identified using historical weather data from Vlieland provided by weatherspark.com from the weather station on de kooy, Vlieland for the 24th of April up to 30th of May, 2021. We used rainfall as the deciding variable to identify rain days on the assumption that it had a more drastic effect on the birds than temperature or wind. Based on the intensity of rainfall, the characterization ranged from light drizzle to a thunderstorm. Thus, we identified rain days as those having at least 4 hours of moderate or higher rainfall within the activity period (between sunrise and sunset) of the Great tit, with 1 being assigned to rain days and 0 to all non-rain days. For the effect of rain on the onset time during incubation, of the three chronotypes, we identified the days immediately after the rain day, named rain-day plus 1 in the dataframe, which was similarly assigned a binary value as the rain days with 1 being the day after the rain and all other days listed as 0.

Statistical analysis

The final data frame consisted of 519 data points with 57 nestboxes, their daily median and onset ranks, final chronotype rank, storm days, the day after the storm, hatching date and days until hatch as a negative scale from first day of incubation till hatch date as 0, fitness measures such as clutch size, number of hatchlings and fledglings and finally whether the nests were successful or not. The continuous chronotype ranks were categorized into early, intermediate and late chronotype groups by dividing an ascending list of the chronotype ranks into 3 parts with 19 nestboxes getting allocated to early, 20 to intermediate and 19 to the late chronotype group.

Effect of Rain

To test the effect of the rain on the birds, a linear mixed effects model was employed in R using the R package Lme4. Onset, Offset and total duration of activity period (calculated as total time spent from onset to last offset) were response variables to be tested. For onset, the day after the rain was modelled as the main effect, while for offset and activity period, the rain day itself was used as we assumed that experiencing the rain would have a greater effect on onset of the bird the next day than the offset. To examine the effect of chronotype on the response to weather, an interaction effect between rain- days and chronotype and the day after the rain and chronotype was also included. To account for the increasing intensity in incubation across all nests as days go on, days until hatch was added as a main effect into all three models as well. Nestbox was added as a random effect for all three models. Onset was modelled as *Onset~DayafterRain + Daysuntilhatch +DayafterRain*Chronotype.Group +1|nestbox* , Offset using *Offset~DayofRain + Daysuntilhatch + DayofRain*Chronotype.Group + 1|nestbox* and activity period as *DailyActivityPeriod~DayofRain + Daysuntilhatch + DayofRain*Chronotype.Group) + 1|nestbox*.

Fitness differences in the chronotypes

To see, irrespective of the rain, whether the chronotypes differed in their fitness, we used the number of fledglings produced as a measure of fitness in a generalised linear model using the glm package in R. We modelled fledglings versus chronotype groups as *fledglings~Chr.Group* describing a poisson family for the response variable.

Results

a) Effect of rain on onset

The early chronotypes were earlier by 9 minutes and 36 seconds on average than intermediate chronotypes whereas late chronotypes were later on average by 13 minutes and 48 seconds, with these timings being largely consistent (figure 1a and table 1). The day after the rain had a significant effect on the onset of the birds where all birds started the day 6 minutes earlier after having faced adverse conditions on the previous day (figure 2a and table1) and the between chronotype trend from earlier is conserved where late chronotypes still have a later onset than intermediate and early chronotypes were still earlier (figure 1b and table 1). There was no effect of rain on the day of the storm (figure 2b).

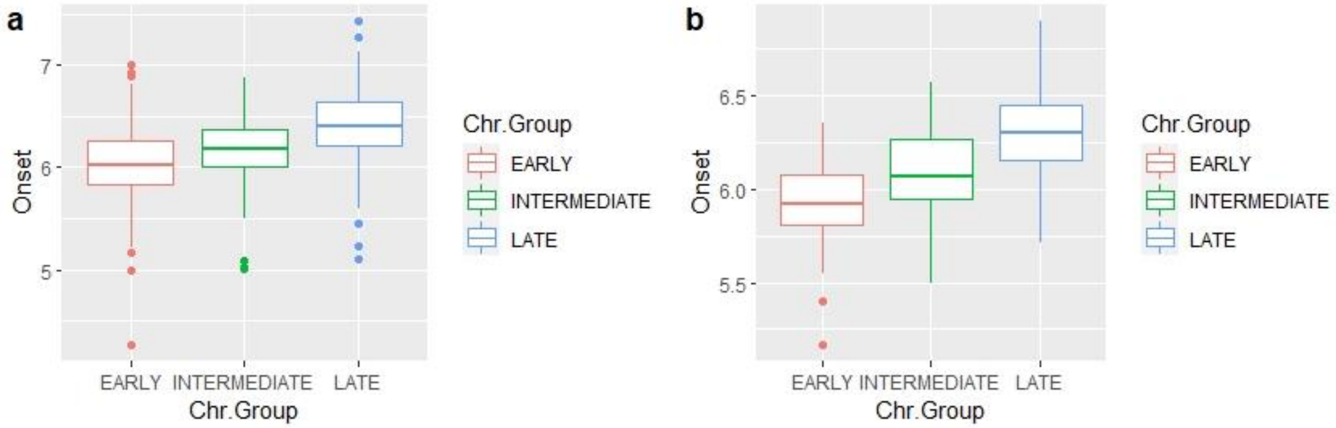

Figure 1a and 1b. 1a) shows the general trend for onset of the chronotypes. It is a boxplot with Onset (time in hours) on the Y axis and the three chronotype groups on the X axis. Early chronotypes wake up earlier than intermediate chronotypes and late chronotypes, later. 1b) The same trend is seen for the chronotypes on days after the rain where early chronotypes wake up earlier than intermediate chronotypes and late chronotypes, later. However overall all three chronotypes have an earlier onset on days after the rain than in general.

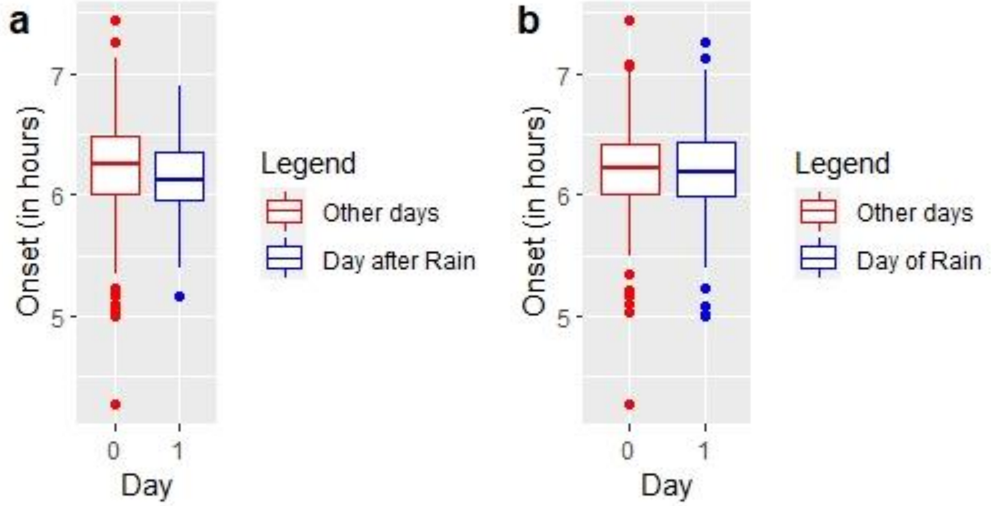

Figure 2a and 2b. 2a Shows a boxplot with Onset (time in hours) on the Y axis, day after the rain in blue and all other days in red on the X axis. 2b Shows a boxplot with Onset (time in hours) on the Y axis, day of the rain in blue and all other days in red on the X axis.

Predictor	**Estimate**	**Std. Error**	**P value**	**Df**
Intercept	6.25	0.05	< 2e-16 ***	112.9
Day after Rain	-0.10	0.05	0.054 *	433.9
Days until hatch	0.01	0.01	0.122	462.5
Early chronotype	-0.16	0.06	0.013 *	61.4
Late chronotype	0.23	0.07	0.001 ***	62.5
Day after rain ^ Early chronotype	-0.01	0.08	0.924	433.5
Day after rain ^ Late chronotype	-0.01	0.08	0.916	431.8

Table 1. Shows a table with the results for the mixed effects model looking at the effect of rain on onset of the birds, using the day immediately after the rain-day. The model was run using the intermediate chronotype group and all days other than day after the heavy rainfall (listed as 0 in the binomial values) as the reference levels. The superscript symbol signifies an interaction effect, triple asterisk for highly significant p value and single asterisk for significance.

b) Effect of rain on Offset

Late chronotypes retired for the evening 22 minutes and 48 seconds later than the intermediate but the early chronotypes did not significantly differ from the intermediate chronotypes in their offset time (figure 3a and table 2). On the rain days however, all birds returned to their nests 15 minutes earlier i.e., had an earlier offset time, as opposed to other days however there is no noticeable difference between the chronotypes (figure 3b, figure 4 and table 2). Additionally, as the birds get closer to the day of hatching, they return to the nest progressively later in the day by 3 minutes per day until day of hatching (table 2).

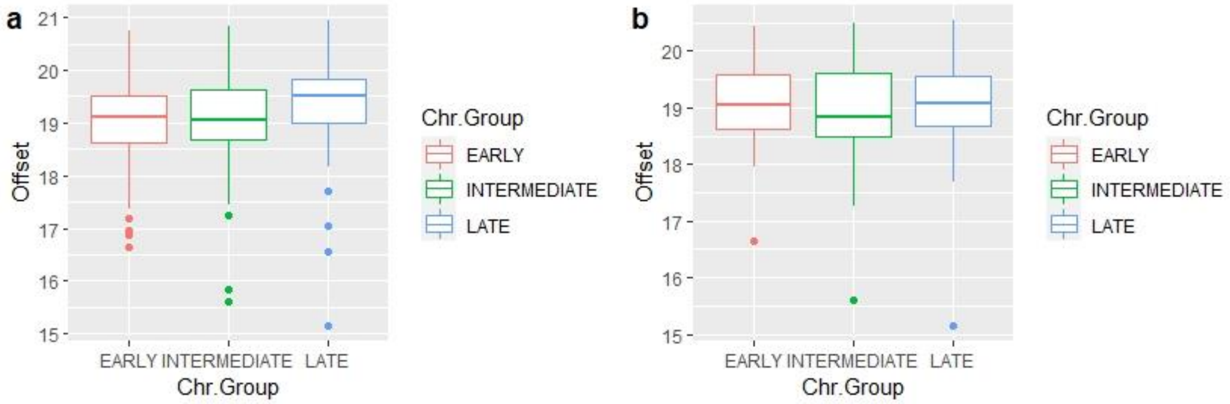

Figure 3a and 3b. 3a shows a boxplot with Offset (time in hours) on the Y axis and the three chronotype groups on the X axis. Late chronotypes return later to the nest as opposed to early and intermediate chronotypes. 2b) shows a boxplot for offset times on the day of rain where in general all three chronotypes returned earlier however there is no noticeable time stratification by chronotype for offset on the day of the storm.

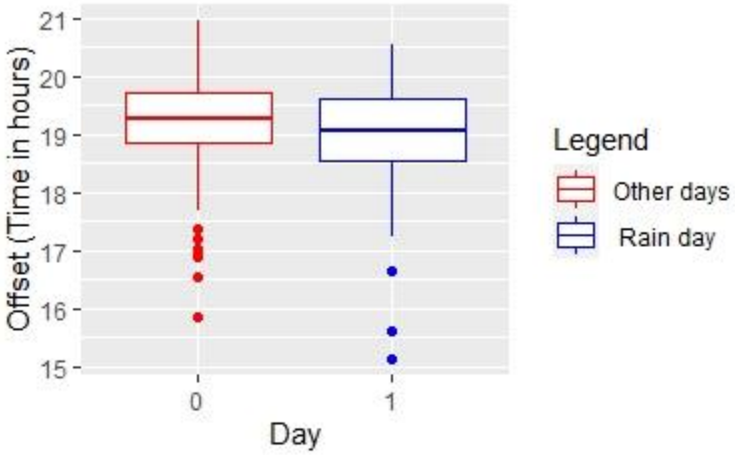

Figure 4. Shows a boxplot with Offset (time in hours) on the Y axis and the rain day on the X axis. All birds returned earlier to the nest on the day of heavy rainfall.

Predictor	**Estimate**	**Std. Error**	**P value**	**Df**
Intercept	19.43	0.12	< 2e-16 ***	85.6
Rain	-0.25	0.10	0.013 *	424.2
Days until hatch	0.05	0.01	3.21e-10 ***	452.3
Early chronotype	-0.14	0.15	0.350	52.8

Late chronotype	0.38	0.15	0.017*	53.7
Rain ^ Early chronotype	0.32	0.17	0.061	429.3
Rain ^ Late chronotype	-0.19	0.15	0.209	425.3

Table 2. Shows a table with the results for mixed effects model for the effect of rain on offset of the birds. The model was run using the intermediate chronotype group and all days other than day of heavy rainfall (listed as 0 in the binomial values) as the reference levels. The superscript symbol signifies an interaction effect, triple asterisk for a highly significant p value.

c)Effect of rain on daily activity period of the birds

The chronotypes did not significantly differ in their total activity period (figure 5). On days of heavy rainfall, total activity period decreases by 10 minutes and 20 seconds, however this was not significant (table 3 and figure 6). However closer to hatching, the total active time increased by 2minutes and daily 24 seconds per day (table 3).

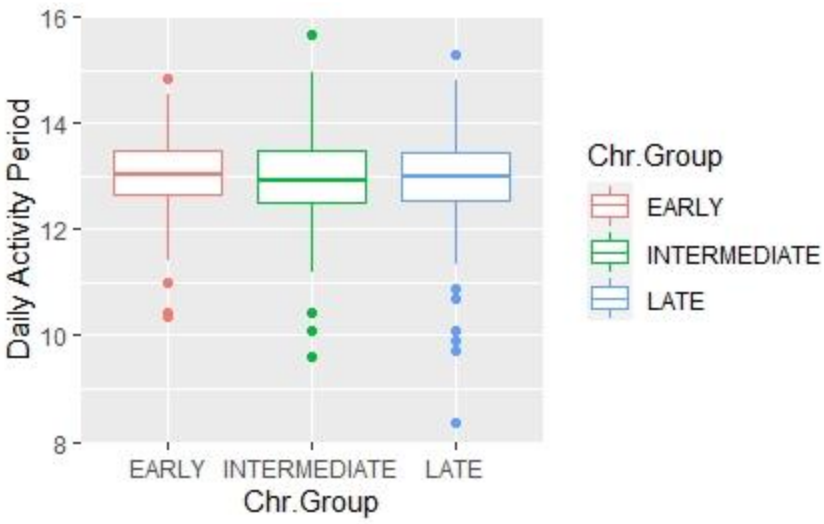

figure 5. Shows a boxplot with the results for mixed effects model for the effect of rain on total daily activity period of the birds (in hours). There is no significant difference between the chronotypes in their total activity period.

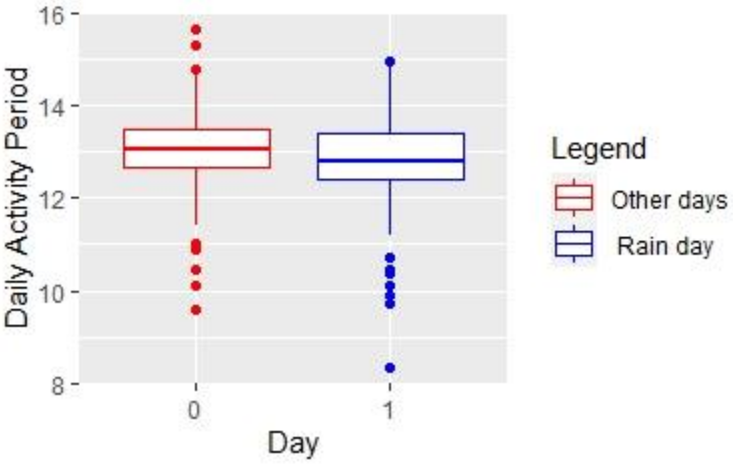

Figure 6. Shows a boxplot with Daily activity period on the Y axis and the rain days on the X axis. Although the birds seem to have returned earlier on the rain-day, this was not significant.

Predictor	**Estimate**	**Std. Error**	**P value**	**Df**
Intercept	13.18	0.12	< 2e-16 ***	91.0
Rain	-0.17	0.11	0.127	424.3
Days until hatch	0.04	0.01	1.07e-06 ***	455.7
Early chronotype	0.03	0.16	0.827	52.8
Late chronotype	0.19	0.16	0.251	53.9
Rain ^ Early chronotype	0.29	0.19	0.127	430.3
Rain^ Late chronotype	-0.28	0.17	0.092	425.6

Table 3. Shows a table with the results for mixed effects model for the effect of rain on total activity period of the birds. The model was run using the intermediate chronotype group and all days other than day of heavy rainfall (listed as 0 in the binomial values) as the reference levels. The superscript symbol signifies an interaction effect, triple asterisk for a highly significant p value.

d)Fitness differences between the chronotypes

There was no significant difference between the three chronotypes on the total number of fledglings produced (table 4 and figure 7).

Predictor	**Estimate**	**Std. Error**	**P value**
Intercept	0.02	0.15	<2e-16 ***
Early Chronotype	0.29	0.22	0.270
Late chronotype	0.35	0.22	0.615

Table 4. Shows a table with the results for the generalized linear model for the effect of chronotype on the number of fledglings. The model was run using the intermediate chronotype group as the reference level. The superscript symbol signifies an interaction effect, triple asterisk for a highly significant p value.

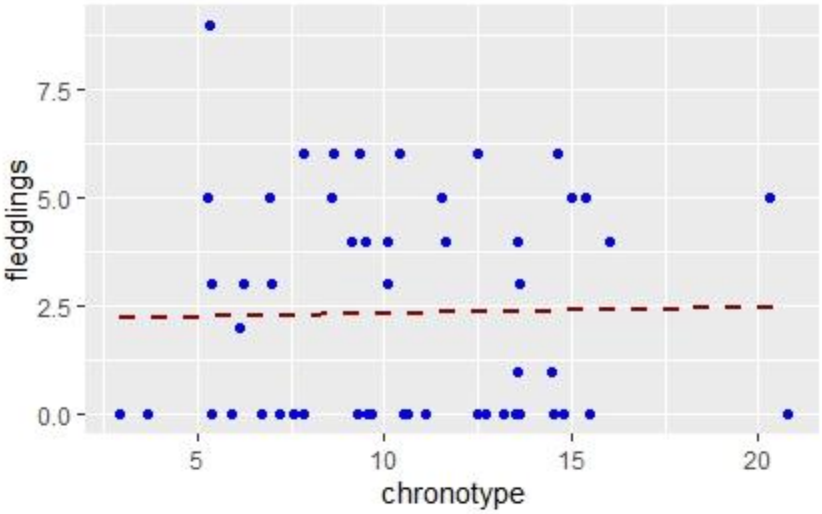

Figure 7. Shows a scatter with number of fledglings on the Y axis and a continuous chronotype on the X axis.

Discussion

Here we show that great tits on Vlieland do indeed exhibit chronological structuring into early, intermediate and late chronotypes with the extremes (early and late) being significantly different from each other in timings (figure 1a and 2a). The birds seem to be more rigid in their onset timings since although all birds started earlier on the day after experiencing heavy rain, the three distinct chronotypes still maintained their previous stratification (Figure 1b). The same cannot be said for offset where although all birds returned earlier on the days of heavy rain, the structuring is not as distinct (figure 2a and 2b). This seems to further solidify the idea that onset timing is more important to great tits that usually nest in holes or cavities with low light levels. This was previously suggested since all major activities such as mate attraction and territory defending, during the breeding period, is done mostly in the morning (Kacelnik and Krebs 1982; Poesel et al 2007, Murphy et al 2008). Our findings also corroborate a previous laboratory study on wild-derived, hand raised birds by Lehmann et al (2012) that found greater sensitivity of activity offset to temperature than activity onset. Hence for both laboratory and field studies, using onset time seems to provide a more robust estimate of chronotype, at least for a passerine such as the great tit.

The activity period, described as the total time spent active between first onset and last offset, seems to be the same across all chronotypes. This suggests that although great tits show different chronotypes, the total activity period is very rigid and conserved for the species, increasing by 2 minutes and 24 seconds per day till hatching (Table 3). This could be a response to changing day length in spring (particularly the month of May) where day length increases at a decreasing rate of 3 minutes in early May up to 2 minutes at the end of May (www.timeanddate.com). This increase in activity period is brought about by retiring later in the day, increased offset time (Table 2), rather than starting earlier in the day (no effect of days until hatch on onset, Table1).

The chronotypes also did not significantly differ in the total number of fledglings produced and fared badly irrespective of chronotype (figure 7). Previous studies on blue tits have found a positive correlation between rainfall and nestling growth (Mainwaring, 2016), however another study in great tits showed that nestlings grew at a reduced rate with some daytime rain above 1millimetre per hour (Keller and Van Noordwijk, 1994). Considering the dire environmental conditions this year (2021), we cannot conclusively corroborate either study other than claim that beyond a threshold all nestlings fare badly and struggle to survive until fledging. This breeding season had high chick mortality rates (indicated by several points under 2 and at 0 on the X axis in figure 7) brought about by low temperatures and heavy rainfall leading to low food supply. Great tits mainly feed on caterpillars growing on the pedunculate oak (*Quercus robur*) which sprouted very late this season, causing a huge shortage in food particularly for the early and middle broods.

These results suggest that using incubation temperature profiles and a ranking of onset and median of activity in free living birds seems to be an efficient way of chronotyping with relative robustness. Although these components for chronotyping are species dependent, an important aspect to consider within our system are age and sex related effects on chronotypes. Steinmeyer et al (2010) found that female blue tits spent longer in the nest box, sleeping, than males and 1st year birds stayed longer in the nestbox after waking up than older birds. The sex related variation in sleep is already accounted for in our system since we use incubation temperature profiles that by and large give us a chronotype of only the female, however age would be an important component to add into the model. Finally, our findings of chronotypes in a free-living bird species invites prospects on future studies on wild species of other phyla in a bid to better understand the persistence of chronotypes in a population and the advantages or disadvantages of being one over the other, in the wild.

Acknowledgements

I would like to thank Barbara Helm and Aurelia Strauss for their guidance and regular supervision, Marcel Visser (NIOO) for the permissions and opportunity to work on this project and Henri and Lies for their assistance in data collection and in making for an enjoyable workplace. Finally, I would like to thank the MEME program and its coordinators without which this project would not have been possible.

References

Álvarez, E. (2014). Incubation and hatching periods in a Mediterranean Great Tit Parus major population. *Bird Study*, 11.

Amin, B., Slabbekoorn, H., Schaaf, M., & Tudorache, C. (2016). "Early birds" take it easy: Diurnal timing is correlated with overall level in activity of zebrafish larvae. *Behaviour*, *153*(13–14), 1745–1762. https://doi.org/10.1163/1568539X-00003376

Atema, E., van Noordwijk, A. J., Boonekamp, J. J., & Verhulst, S. (2016). Costs of long-term carrying of extra mass in a songbird. *Behavioral Ecology*, *27*(4), 1087–1096. https://doi.org/10.1093/beheco/arw019

Capilla-Lasheras, P. (n.d.). *IncR: a new R package to analyse incubation behaviour*. 8.

Diez-Me, D., Jose, J., & Barba, E. (2021). *Impacts of ambient temperature and clutch size on incubation behaviour onset in a female-only incubator songbird*. 16.

Facer-Childs, E. R., Boiling, S., & Balanos, G. M. (2018). The effects of time of day and chronotype on cognitive and physical performance in healthy volunteers. *Sports Medicine - Open*, *4*(1), 47. https://doi.org/10.1186/s40798-018-0162-z

Griffith, S. C., Mainwaring, M. C., Sorato, E., & Beckmann, C. (n.d.). *Development and lead to earlier hatching in a passerine bird*. 14.

Gwinner, H., Capilla-Lasheras, P., Cooper, C., & Helm, B. (2018). 'Green incubation': Avian offspring benefit from aromatic nest herbs through improved parental incubation behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1880), 20180376. https://doi.org/10.1098/rspb.2018.0376

Helm, B., & Visser, M. E. (2010). Heritable circadian period length in a wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1698), 3335–3342. https://doi.org/10.1098/rspb.2010.0871

Keller, L F., Van Noordwijk, A J. (1994). Effects of local environmental conditions on nestling growth in the great tit Parus major L. *Ardea,* 82(2):349-362. https://doi.org/10.5167/uzh-53659

Labyak, S. E., Lee, T. M., & Goel, N. (n.d.). *Rhythm chronotypes in a diurnal rodent, Octodon degus*. 9.

Lehmann, M., Spoelstra, K., Visser, M. E., & Helm, B. (2012). Effects of Temperature on Circadian Clock and Chronotype: An Experimental Study on a Passerine Bird. *Chronobiology International*, *29*(8), 1062–1071. https://doi.org/10.3109/07420528.2012.707159

Mainwaring, M. C. (2016). Local weather conditions have complex effects on the growth of blue tit nestlings. *Journal of Thermal Biology*, 8.

Nikhil, K. L., Abhilash, L., & Sharma, V. K. (2016). Molecular Correlates of Circadian Clocks in Fruit Fly *Drosophila melanogaster* Populations Exhibiting *early* and *late* Emergence Chronotypes. *Journal of Biological Rhythms*, *31*(2), 125–141. https://doi.org/10.1177/0748730415627933

Nord, A., & Cooper, C. B. (2020). Night conditions affect morning incubation behaviour differently across a latitudinal gradient. *Ibis*, *162*(3), 827–835. https://doi.org/10.1111/ibi.12804

Nord, A., Nilsson, J.-Å., Rio, A. E. C. M. D., & McPeek, E. M. A. (n.d.). *Incubation Temperature Affects Growth and Energy Metabolism in Blue Tit Nestlings*. 000.

Nur, N. (1984). Feeding frequencies of nestling blue tits (Parus caeruleus): Costs, benefits and a model of optimal feeding frequency. *Oecologia*, *65*(1), 125–137. https://doi.org/10.1007/BF00384475

Öberg, M., Arlt, D., Pärt, T., Laugen, A. T., Eggers, S., & Low, M. (2015). Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and Evolution*, *5*(2), 345–356. https://doi.org/10.1002/ece3.1345

Podlas, K., & Richner, H. (n.d.). Partial incubation and its function in great tits (Parus major)—An experimental test. *Behavioral Ecology*, 7.

Refinetti, R., Earle, G., & Kenagy, G. J. (2019). Exploring determinants of behavioral chronotype in a diurnal-rodent model of human physiology. *Physiology & Behavior*, *199*, 146–153. https://doi.org/10.1016/j.physbeh.2018.11.019

Rittenhouse, J. L., Robart, A. R., & Watts, H. E. (n.d.). *Variation in chronotype is associated with migratory timing in a songbird*. 5.

Roenneberg, T., Kuehnle, T., Juda, M., Kantermann, T., Allebrandt, K., Gordijn, M., & Merrow, M. (n.d.). *Epidemiology of the human circadian clock$*. 10.

Roenneberg, T., Wirz-Justice, A., & Merrow, M. (n.d.). *Life between Clocks: Daily Temporal Patterns of Human Chronotypes*. 12.

Roulin, A. (2002). *SHORT- AND LONG-TERM FITNESS CORRELATES OF REARING CONDITIONS IN BARN OWLS TYTO ALBA*. 10.

Royzrakh-Pasternak, E., Dayan, T., Levy, O., & Kronfeld-Schor, N. (n.d.). *Early birds, late owls, and the ecological role of intra-population chronotype variation*. 19.

Sanz, J. J. (1999). Energy expenditure, nestling age, and brood size: An experimental study of parental behavior in the great tit Parus major. *Behavioral Ecology*, *10*(5), 598–606. https://doi.org/10.1093/beheco/10.5.598

Schöll, E. M., Aparisi, M. P., & Hille, S. M. (2020). Diurnal patterns of ambient temperature but not precipitation influence incubation behavior in Great Tits. *Journal of Ornithology*, *161*(2), 529–538. https://doi.org/10.1007/s10336-019-01737-9

Simmonds, E. G., Sheldon, B. C., Coulson, T., & Cole, E. F. (2017). Incubation behavior adjustments, driven by ambient temperature variation, improve synchrony between hatch dates and caterpillar peak in a wild bird population. *Ecology and Evolution*, *7*(22), 9415–9425. https://doi.org/10.1002/ece3.3446

Smith, C. S., Folkard, S., Schmieder, R. A., Parra, L. F., Spelten, E., Almiral, H., Sen, R. N., Sahu, S., Perez, L. M., & Tisak, J. (2002). Investigation of morning–evening orientation in six countries using the preferences scale. *Personality and Individual Differences*, 20.

Steinmeyer, C., Schielzeth, H., Mueller, J. C., & Kempenaers, B. (2010). Variation in sleep behaviour in free-living blue tits, Cyanistes caeruleus: Effects of sex, age and environment. *Animal Behaviour*, *80*(5), 853–864. https://doi.org/10.1016/j.anbehav.2010.08.005

Tauber, E. (2015). Gene expression associated with early and late chronotypes in Drosophila melanogaster. *Frontiers in Neurology*, *6*, 9.

Wicht, H., Korf, H.-W., Ackermann, H., Ekhart, D., Fischer, C., & Pfeffer, M. (2014). Chronotypes and rhythm stability in mice. *Chronobiology International*, *31*(1), 27–36. https://doi.org/10.3109/07420528.2013.820739