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Karagicheva, Julia; Rakhimberdiev, Eldar; Saveliev, Anatoly; Piersma, Theunis

Functional Ecology

DR JULIA KARAGICHEVA (Orcid ID : 0000-0002-2404-6826)

DR ELDAR RAKHIMBERDIEV (Orcid ID : 0000-0001-6357-6187)

Corresponding author mail id : jkaraj@gmail.com
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Annual chronotypes functionally link life histories and life cycles in birds

Julia Karagicheva[1], Eldar Rakhimberdiev[1,2], Anatoly Saveliev[3] & Theunis Piersma[1,4]

[1]*NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems and Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands*

[2]*Department of Vertebrate Zoology, Biological Faculty, Lomonosov Moscow State University, 119991, Moscow, Russian Federation*

[3]*Institute of Ecology and Geography, Kazan Federal University, Kazan, Russian Federation*

[4]*Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands*

Abstract

1. Life-history responses to ecological selection pressures can be described by a slow-fast life-history axis. Along this axis, fast-living animals usually invest in high breeding output, while slow-living ones prioritize their own survival.

2. Birds may solve the trade-off between reproduction and survival by optimising their seasonal schedules. Breeding early tends to facilitate reproductive success, whereas breeding late increases the chances to survive. On the basis of this argument, short- and long-lived birds should benefit from initiating spring activities earlier and later, respectively.

3. The timing of seasonal activities, all else being equal, depends on the architecture of endogenous circannual clocks. Particularly, the length of the circannual period relative to the 365-day environmental year facilitates either the anticipation of seasonal activities (in case of periods shorter than 365 days) or represents a responsive mode (when periods are longer than 365 days). The two alternatives will be manifested by early or late annual chronotypes, respectively.

4. We hypothesise that, in birds, annual chronotype will correspond with position on the 'pace-of-life scale'. Species with low survival probability, and thus a poor chance of breeding in a next season, should show early annual chronotypes facilitated by circannual clock periods shorter than 365 days. In contrast, species with high survival rates should benefit from relatively long circannual periods.

5. We predicted that circannual period lengths should correlate positively with species-specific adult annual survival rates. Using published data for 16 wild bird species, we confirmed the predicted correlation. In our analysis, we accounted for the possible metabolic nature of circannual clocks, a correlation between rate of metabolism and survival, and phylogenetic relationships.

6. Based on our finding, we propose that evolutionary responsive circannual clocks help birds cope with temporal variation in environment in ways that are most appropriate for their life-history and life-table attributes.

Key words: annual chronotype, circannual rhythm, life-cycle stage, metabolic rate, pace of life, reproduction versus survival trade-off, seasonal migration, slow-fast life-history continuum

Introduction

Time runs at different paces for fast- and slow-living organisms (Helm & Shavit, 2017). The 'pace-of-life' of organisms is reflected in the position on a virtual slow-fast life-history continuum (Ricklefs & Wikelski, 2002; Versteegh, Schwabl, Jaquier, & Tieleman, 2012). Along the continuum, fast-living organisms tend to be smaller, mature faster, reproduce at a higher rate, and have shorter lifespans than slow-living ones. The continuum is the result of correlated variations in organismal rate processes along multiple physiological and behavioural axes, which include growth, metabolism, sexual maturation, learning and competitive risk-taking (Bielby *et al*., 2007; Reale *et al*., 2010; Ricklefs & Wikelski, 2002). When the rate processes are not intercorrelated, they are often complementary or compensatory to each other (Glazier, 2015). Such adaptive coordination facilitates an optimal match between internal and environmental conditions (Glazier, 2015; Ricklefs & Wikelski, 2002).

The adaptively coordinated rate processes in an organism form its unique life-history strategy of allocating resources among competing fitness components, especially reproduction and survival (McGraw & Caswell, 1996; McNamara, Welham, Houston, Daan, & Tinbergen, 2004; Orzack & Tuljapurkar, 2001; Sæther & Bakke, 2000). In birds, and

perhaps especially in seasonally migrating populations, the reproduction-survival trade-off is often mediated by time of a season: early breeding usually facilitates high reproductive outcome, but entails higher risks of death due to challenging weather, possible starvation due to insufficient body stores, or the risk of predation (see Drent, Both, Green, Madsen, & Piersma, 2003; Møller, 1994 for empirical examples, and Harts, Kristensen, & Kokko, 2016; Kokko, 1999; Kristensen, Johansson, Ripa, & Jonzén, 2015 for theoretical background). In contrast, breeding late is safer in terms of survival, but often decreases reproductive output (Lok, Veldhoen, Overdijk, Tinbergen, & Piersma, 2017; Weiser *et al.*, 2017). Thus, a relatively early induction of spring activities should be beneficial for species with "fast" life-histories, for which fitness depends on instantaneous reproductive success rather than a long life. The opposite should hold for birds with "slow" life histories. Therefore, when survival-reproduction trade-off is mediated by timing of breeding, resource allocation to either fitness component can be optimised by fine-tuning the timing of spring activities, as it is often found in birds breeding in seasonal environments at temperate and northern latitudes (Drent & Daan, 1980; Helm & Lincoln, 2017; Karagicheva, Liebers, *et al.*, 2016; Öberg, Pärt, Arlt, Laugen, & Low, 2014).

Spring activities, such as pre-flight fuel storage, pre-alternate moult of plumage, migratory restlessness, and the actual migratory flight, are triggered by environmental cues or *Zeitgebers* such as photoperiod, phenology or social interactions (van Wijk, Schaub, & Bauer, 2017; Williams, 2012; Bradshaw & Holzapfel, 2007; Dawson, 2008, 2015; Helm, Piersma, & van der Jeugd, 2006), Nevertheless, circannual clocks also play a crucial role in their timing (Gwinner 1986). Circannual clocks are endogenous oscillator systems suggested to be driven either by whole organism metabolism (Wikelski *et al.*, 2008) or by cyclic gonadal activity (Dawson, King, Bentley, & Ball, 2001). The clocks have a period of about 12 months, but usually run ahead or behind; they need systematic resetting by external time

cues (Gwinner 1986). In the absence of relevant cues, such as under experimental conditions, circannual clocks are not reset and run free with a wide range of periods (to our knowledge, from 6 to 18 months; see Gwinner 1986). Under constant photoperiod and temperature, some seasonal activities are exerted spontaneously, at approximately the same phase of circannual cycle as when entrained to environmental cues (reviewed in Gwinner, 1986; Helm, Schwabl, & Gwinner, 2009).

Whether exposure to environmental cues will facilitate or delay exertion of seasonal activities largely depends on the period-length relationship between the circannual oscillator and the environmental cycle (in this case: year). According to the phase-period rule, deviation of intrinsic periods from environmental cycles, i.e. the cycles of environmental *Zeitgebers,* will affect the rate of entrainment (cue-response) and determine whether the animal has an early or a late chronotype (Helm *et al*., 2017; Helm & Lincoln, 2017; Roenneberg, Daan, & Merrow, 2003). A number of factors can affect the rate of entrainment, but in general, organisms with relatively short intrinsic cycles will be early and the ones with long cycles will be late (Floessner & Hut, 2017; Roenneberg *et al*., 2003). Thus, animals with circannual periods shorter than 12-months will exert early 'annual chronotypes', and be prepared to initiate seasonal activities even before the environment becomes 'ready'. In this case, external cues will prevent seasonal activities from being triggered too early (see Fig. 1 in Chandola-Saklani, Thapliyal, Negi, Diyundi, & Choudhary, 2004 for an example). With circannual periods longer than the environmental cycle, physiological changes in the organism will lag behind the seasonal development of the environment. As a consequence, external cues will have to facilitate the timely expression of physiological change.

We hypothesised that when timing of activities is shaped by long-term survival perspectives, short- and long-lived birds will increase their fitness by earlier or later responses to seasonal cues and will thus benefit from having short and long circannual

periods, respectively. We therefore predict that, in birds, annual chronotype should correlate with species-specific annual survival probability in the wild. To test this prediction, we compiled available published data on (1) the lengths of circannual period expressed under constant photoperiodic conditions indoors, and (2) species-specific adult annual survival rate. We then calculated the deviation of the circannual-period lengths from the 365-days environmental year and regressed the resulting representation of circannual chronotype on annual survival rate, taking into account the notion that metabolic rate correlates with both survival and circannual chronotype due to the possible metabolic nature of circannual clocks. A possible effect of shared ancestry was accounted for by including a phylogenetic correlation in the model. We discuss our results from an ecological perspective and suggest a theoretical explanation for the variation in circannual period length along the slow-fast life-history axis in birds. To our knowledge, this is the first comparative study linking the features of circannual clocks with life-history traits.

Methods

We assembled published data on free-running circannual periods for birds maintained under experimentally fixed photoperiodic and temperature conditions in captivity. Our sample included 14 species of songbirds (order Passeriformes) and two shorebird species (order Charadriiformes), the red knot *Calidris canutus* and the great knot *C. tenuirostris* (available as Appendix S1 and at https://git.io/vAuyo). We had to limit our dataset to species for which data on both circannual periods and annual survival rates were available. The published data on circannual periods were found by browsing for the term "circannual" and its synonyms in www.scholar.google.com, using reference lists in books, and by screening publications of authors specialized in chronobiology.

Data on circannual periods were available either as reported values for individual birds or as published diagrams of changes in the physiological parameters of different individuals over time. In the latter case, the beginning and the end dates of each period were estimated from the time axis of the graphic. If we had a choice of data collected in various photo-regimes, we selected for datasets from those experiments where photo-regime was kept close to 12:12 LD (12 hours light/12 hours dark). The circannual period lengths were estimated, for each individual, as the intervals between onset dates of a life-cycle stage (seasonal activity) in successive years. However, it is often impossible to unequivocally define the onset dates, since some measurements can fluctuate for many reasons. In such cases we had to apply rules of thumb. When estimating gonadal cycles from the graphics, we defined the initiation date as the time-point at which growing gonads reached a size of 2 mm (Gwinner 1981). For pre-migratory body mass peaks, the onset dates were defined as the time-point at which at body mass started to steadily increase to reach maximal value.

The data included circannual periods for all available life-cycle stages. However, circannual period lengths often change in the course of the cue-deprived treatment (Gwinner, 1986; Karagicheva, Rakhimberdiev, *et al*., 2016), and most of the circannual period lengths were available for the first one or two years spent under experimental conditions. We therefore limited our sample to transitory cycles during which the animals were transferred from natural to constant photoperiods (cycle 0), and the first cycle (cycle 1) when animals were exposed to a constant photoregime the whole year (Table 1).

We calculated deviations of circannual periods from the calendar year (hereafter, circannual deviation) for each available life-cycle stage by subtracting 365 days from the observed duration of a circannual cycle (Table 1). The species-specific adult annual survival rates in the wild (Appendix S2 and at https://git.io/vAuSe), metabolic rates (Appendix S3 and https://git.io/vAuSZ) and body mass (Appendix S4 and at https://git.io/vAuSB) were

searched for in www.scholar.google.com and in an on-line database (*COMADRE Animal Matrix Database*, 2015). If several values per species were available, we used their median in the analysis (Table 1). Survival rates of crossbills *Loxia curvirostra* were likely to be biased low because crossbills are irruptive with low site fidelity, and thus difficult to resight or recapture (Alonso & Arizaga, 2013).

Although time-keeping may differ between sexes (Hau *et al*., 2017; Rani & Kumar, 2013), we were not able to account for this possibility as sex of experimental birds was unknown in six of the 16 species, while in nine species only males were used in the experiments. As there was no obvious trend in the proportion of males versus unknown sex along the annual survival axis, we opted not to include sex as a variable in our model.

The species in our study had an almost 20-fold range in body masses, from 8 g in the common chiffchaff *Phylloscopus collybita* to 150 g in the great knot (see Appendix S4). In comparative studies looking for functional links between longevity and other traits across species, it is generally recommended to account for species-specific body mass to eliminate the part of the correlation caused by the allometric relationship between most organismal processes and body mass (Speakman, 2005). However, organismal processes involved in time-keeping are energy- rather than mass-related (Riede, van der Vinne, & Hut, 2017; Speakman, 2005; Wikelski *et al*., 2008). Since, in our dataset (Appendix S5 and at https://git.io/vAu9I), basal metabolic rate (BMR) correlated with body mass, we used BMR to account for the body-size effect. Following Speakman (2005), we regressed the circannual deviation and annual survival rate (log-transformed, natural logarithm) on the values of BMR (also log-transformed, natural logarithm) published for the 16 species (Table 1) and used the residuals as the response and explanatory variables, respectively, in models testing for the correlation between the two traits.

To control for phylogenetic autocorrelation in the analysis (Harvey & Pagel, 1991; Speakman, 2005), we introduced a phylogenetic variable in the models. We accounted for phylogenetic uncertainty (Huelsenbeck, 2000) by generating 10,000 trees with different topologies for all species in our dataset based on a comprehensive bird phylogeny for 9993 species (Hackett 'All Species' from Jetz, Thomas, Joy, Hartmann, & Mooers, 2012), using an online phylogeny generating tool (available at http://birdtree.org/). Different trait-evolution models require specific statistical approaches, we tested whether Brownian or Ornstein-Uhlenbeck models best fitted the data. Here, we used fitContinuous function from geiger package (Harmon, Weir, Brock, Glor, & Challenger, 2008) in an R statistical environment (R Core Team, 2017). We collected AIC (Akaike information criterion, Akaike, 1974) values for the regressions of each evolutionary model applied to each of the 9999 phylogenetic trees. We then calculated ΔAIC, pairwise, between the evolutionary models, for each tree. Based on the distribution of 9999 ΔAIC values (mean ΔAIC 0.48 ± 0.53), Brownian and Ornstein-Uhlenbeck models were equally supported. Given that analyses based on small sample sizes tend to spuriously support the more complex Ornstein-Uhlenbeck model (Cooper, Thomas, Venditti, Meade, & Freckleton, 2016), we assumed that Brownian evolution model adequately suited our data and were thus able to use for model fitting MCMCglmm R package (Hadfield, 2010; Hadfield & Nakagawa, 2010).

We assessed the relationships among the circannual deviation, species-specific annual survival rate, and time spent in a constant photoregime (cycle 0 versus cycle 1), controlling for random effects of individuals, species, seasonal activities and studies. To do so we fitted Bayesian mixed models in the package MCMCglmm in R. To account for the uncertainty in phylogenetic relationships, we first randomly sampled 100 trees from the downloaded 9999 phylogenetic trees. Since MCMCglmm handles only one phylogenetic tree per model, we further incorporated the subset in 100 MCMCglmm models within the package mulTree

(Guillerme & Healy, 2017; Gutiérrez, Rakhimberdiev, Piersma, & Thieltges, 2017).

Technical information on the model parameters used and the replicable code are provided in

Appendix S6 (https://git.io/vAELZ).

We used DIC (deviance information criterion by Spiegelhalter, Best, Carlin, & van

der Linde (2002) for model selection. Following Zuur, Ieno, & Smith (2007), we started

model selection from the most complete model:

$Deviation_{BMR}$ ~ $Survival_{BMR}$ + $Cycle\_number$ + $Survival_{BMR}$:$Cycle\_number$

random effects: LCS+study+species+species:BirdID + pedigree,

where $Deviation_{BMR}$ is the circannual deviation corrected for species-specific BMR,

$Survival_{BMR}$ is the effect of species-specific annual survival rate corrected for species-specific

BMR, *Cycle_number* distinguishes between the effects of transitional cycle and the cycle

fully undergone under experimental photoregime, $Survival_{BMR}$:$Cycle\_number$ is an

interaction term. *Species:BirdID*, *LCS*, *study*, *species* and *pedigree* define random effects for

the: individual bird, life-cycle stage, study, from which the data were retrieved, bird species

and phylogenetic variable, respectively. None of the random effects are nested within each

other.

We calculated an analogue of Pagel's *λ,* or phylogenetic signal (the amount of variance

explained by the phylogeny compared to the total amount of among species variance), of

annual chronotype as *var(phylogenetic)/(var(phylogenetic)+var(species)),* phylogenetic

variance contribution (the amount of variance explained by the phylogeny compared to the

total variation in the data) following Bulla *et al*. (2016) as:

var(phylogenetic)/(var(phylogenetic)+var(BirdID)+var(LSC)+var(study)+var(species)+var(residual)),

with an intra-specific agreement repeatability as:

var(species)/(var(species)+var(phylogenetic)+var(BirdID)+var(LSC)+var(study)+
var(residual)),

and the adjusted repeatability as: *var(species)/(var(species)+ var(residual))* following (Nakagawa & Schielzeth, 2010).

A small sample size may cause bias in a model accounting for phylogeny (Garamszegi & Møller, 2010). Thus, we provide code and an output of an MCMCglmm model of the same parameter structure, but not including the phylogenetic variable, in Appendices S6 and S7 (https://git.io/vAELZ and https://git.io/vAuHK).

Results

Deviation of circannual periods in the species included in this study varied between 170 and 635 days, with a mean value of 371 days, and annual survival rates ranged from 0.28 to 0.90 with a mean = 0.62. Consistent with our prediction, the BMR-adjusted circannual periods were longer in species with higher BMR-adjusted annual survival rates. The correlation slope was steeper during the transition from the natural to an unvarying photoperiod (cycle 0: *mean slope estimate* = 215.1 days, 95% credible interval between 63.8 and 369.5 days) than the first cycle under such conditions (cycle 1: *mean slope estimate* = 133.4 days, 95% credible interval between -13.9 and 282.0 days; Fig. 1, Appendix S7 https://git.io/vAuHK). The difference in slopes between cycle 0 and cycle 1 was statistically significant, as indicated by $\Delta DIC = 8.2$, and, therefore, the full set of parameters was also the best one (Appendix S7). The phylogenetic signal λ for circannual period length was 0.81 and the phylogenetic variance contribution was 0.43. The adjusted and agreement intra-specific repeatabilities of the trait were 0.95 and 0.10, respectively. The slope of correlation between annual survival rate and circannual period and its statistical significance were similar in the models that

included or did not account for phylogenetic effect (cycle 0: *mean slope estimate* = 200.2 days, 0.95% credible interval between 73.3 and 331.8 days; cycle 1: *mean slope estimate* = 120.3 days, 95% credible interval between − 0.04 and 247.2 days, Appendix S7).

Discussion

It has long been known that free-running circannual periods in living organisms vary in length and rarely match the 365-day year (Gwinner, 1986). However, it was only recently proposed that the variation in circannual periods is adaptive; polymorphism in annual chronotypes facilitates a good match between the life histories and environments of organisms (Helm et al., 2017; Helm & Lincoln, 2017; Helm & Shavit, 2017). Here, we, for the first time, provide correlative evidence suggesting that annual chronotypes are the outcome of endogenous-clock properties having been adjusted to selective environments. We test the hypothesis that deviations of the circannual-clock cycle from the calender year actually reflect solutions for the timing-mediated life-history trade-offs.. Consistent with our hypothesis, circannual periods were shorter in the species with lower probabilities of annual survival.

Our analysis was limited to migratory birds breeding in temperate and Arctic zones of the northern hemisphere. Selection pressures on the fitness components can be differently distributed along the time-axis, depending on migratory strategy or geographic and climatic factors for example (Jonzén, Hedenström, & Lundberg, 2007; Kristensen *et al*., 2015). Thus, it is possible that the patterns reported here will not be upheld for resident bird populations, or for species breeding in the southern hemisphere or in the tropics (Newton & Brockie, 2008; Winkler, Ringelman, *et al*., 2014; Young, 1994). Nevertheless, it seems unlikely that annual chronotypes will not work in concert with other life-history correlates, as long as there are seasonal selection pressures on fitness parameters.

Variable circannual periods

In nature, variable environmental conditions require plasticity in life-history strategies (West-Eberhard, 2003). For this reason, the mechanisms coordinating organismal and environmental processes such as stress response or circadian chronotype may vary in the course of development, adjusting to environmental conditions experienced by individuals (Del Giudice, Ellis, & Shirtcliff, 2011; Roenneberg *et al.*, 2004). As a consequence, the coordinating mechanisms will also vary among individuals with different backgrounds or going through different ontogenetic and life-cycle stages. Our study, as well as many previous studies on circannual rhythms in birds (Helm, 2006), revealed high variation in circannual-period lengths among individuals of the same species, but also within each individual. For instance, in shorebirds, circannual periods of spring activities were closer to 365 days than the periods of activities expressed later in the season (Karagicheva, Rakhimberdiev, *et al.*, 2016; Piersma *et al.*, 2008). Karagicheva, Rakhimberdiev, *et al.* (2016) suggested that variations in the precision of expression of circannual cycles in different traits reflect selection pressures for precise timing changing with season.

Timing-dependent selection pressures will also vary with life style. For example, short circannual periods (and early chronotypes) should be useful for the opportunistically breeding red crossbill *Loxia curvirostra*, as they have to be alert to environmental cues almost year-round to opportunistically prepare for nesting as soon as pine cones become available as a food source (Hahn, 1998). In house sparrows *Passer domesticus* (not included in the analysis), the average circannual periods exerted in 12:12 LD are relatively short (10 months according to Wikelski *et al.*, 2008) for a species annual survival rate of 0.55 (Siriwardena *et al.*, 1999). Such a short circannual period is consistent with gonadal recrudescence starting in late autumn in house sparrows, perhaps an adaptation to high territorial competition in a sedentary bird (Hegner & Wingfield, 1986). In contrast, precise

timing will be particularly important for long-distance migrants, and especially extreme "long-jump" migrants, of which Arctic-breeding shorebirds are a typical example (Åkesson *et al*., 2017; Bazzi *et al*., 2016; Conklin, Senner, Battley, & Piersma, 2017; Helm, Gwinner, & Trost, 2005; Piersma, 1987). For these species, environmental cues at departure from equatorial or temperate wintering sites are uninformative of the phenological conditions at remote Arctic breeding grounds (Piersma, *et al*., 1990; Winkler, Jørgensen, *et al*., 2014). To time their spring migration, these shorebirds largely rely on endogenous clocks, which have shown to be remarkably individually precise both in the wild as under unvarying photoperiodic conditions in captivity (Conklin, Battley, & Potter, 2013; Karagicheva, Rakhimberdiev, *et al*., 2016).

The high variation in circannual deviations was well captured by the set of random variables included in our model. As a result, the unexplained (residual) variance was low, which caused the values of phylogenetic signal and intra-specific repeatability to be high when they were calculated accounting for the residual variance only, and contrastingly low when all random variance was taken into account. The difference suggests that circannual chronotype is a heritable, but highly variable, trait. However, we suggest caution when interpreting the phylogeny-related results in this paper, as our analysis was based on a small sample of 16 species from two orders (Garamszegi & Møller, 2010). The phylogenetic correlation was included in the model only to ensure that the hypothesised correlation was not confirmed spuriously due to bias from shared ancestry. Our key finding was that even when shared ancestry was accounted for, the correlation between length of circannual period and annual survival rate remained significant.

Annual chronotype as a life-history covariate

Self-sustaining physiological oscillations of different periodicity in organisms, such as circadian, lunar, tidal or circannual rhythms, play an important role in coordinating rate processes (Hut, Paolucci, Dor, Kyriacou, & Daan, 2013; Neill, 2013; Numata & Helm, 2014; Riede *et al.*, 2017). While circannual oscillations are affected and probably even driven by internal metabolic processes (Wikelski *et al.*, 2008), they are also responsive to external information on environmental seasonal state received from the cue-response systems (Gwinner, 2003; Hahn & MacDougall-Shackleton, 2008). On this basis, we hypothesised that annual chronotypes of migratory birds should correlate with their other life-history traits, and specifically with species-specific annual survival probabilities. Despite vast variation in circannual periods for reasons of individuality, life-style, environment and ancestry (discussed above), we captured this relationship in the assembled data.

Our results extend the view that endogenous rhythms interact with external cues to ensure optimal adjustment of organisms to environments by modulation of the rate of entrainment of endogenous cycles to environmental oscillations (Floessner & Hut, 2017; Helm *et al.*, 2017; Helm & Lincoln, 2017). We projected circannual chronotypes on the slow-fast life-history axis and showed how the flexible system of endogenous oscillations helps birds to cope with temporal variation in environment in ways that are most appropriate for their life-history and life-table attributes. We propose that physiological circannual clocks, being responsive to the endogenous organismal and environmental processes at the same time, can be a physiological mediator coordinating energy in metabolic processes with survival and other organismal properties by adjusting them to external conditions through physiological and behavioural responses.

Authors' contributions

J.K. assembled data and performed the statistical analyses. E.R. and T.P. participated in the concept development. E.R. and A.S. advised on the analyses. J.K. and T.P. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

Data, reproducible R-code and model results is also maintained on GitHub (https://github.com/JKaragicheva/Circannual_cycles) and publicly archived at https://doi.org/10.5281/zenodo.1250826.

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SUPPORTING INFORMATION

Table S1 Circannual cycle lengths

Table S2 Species-specific annual survival rates

Table S3 Species-specific basal metabolic rates

Table S4 Species-specific body mass

Figure S5 Correlation BMR body mass

Appendix S6 R code

Table S7 MCMCglmm models output

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Table 1. The circannual deviations from 365 days (mean and SD of the raw data points that were used in the analysis) and details on the experimental setups; species-specific annual survival probability and BMR.

Species	Number of individuals used in the experiment	Circannual deviation, days (mean ± SD)	Cycles since transition to unvarying photoregime	Photoperiod	Annual survival rate (median)	BMR, W	Body mass, g
Ficedula albicollis	10 males	28.6 ± 22.2 [1]	0,1	13:11 LD	0.45 [14]	0.276[34]	14.2 [14]
Ficedula hypoleuca	7 males	36.3 ± 25.8 [1]	0,1	12:12 LD	0.48 [15]	0.230[35]	11.6 [14]
Fringilla coelebs	15 males	53.5 ± 37.4 [2]	1	12:12 LD	0.6 [16, 17]	0.373[30]	24.2 [30]
Fringilla montifringilla	2 males	90.0 ± 34.6 [3]	1	10:14 LD	0.57 [18]	0.516[31]	24.1 [31]
Junco hyemalis	7 males	100.4 ± 83.6 [4]	1	24 DD	0.49 [14]	0.192[31]	19.6 [14]
Loxia curvirostra	3 males	- 71.6 ± 54.2 [5, 6]	1	12:12 LD	0.45 [19,20]	0.600[30]	40.6 [30]
Phylloscopus trochilus	6 unknown	- 22.3 ± 25.2 [7, 8]	0,1	12:12 LD	0.34 [16,21,22,23]	0.208[30]	9.4 [30]
Phylloscopus collybita	7 unknown	- 10.0 ± 18.0 [8]	0	12:12 LD	0.28 [16,22]	0.165[30]	7.7 [30]
Parus cristatus	8 unknown	- 46.3 ± 17.8 [6]	0,1	10:14 LD	0.6 [14,24]	0.470[14]	11.2 [14]
Passer montanus	3 females	- 87.0 ± 66.6 [6]	0,1	10:14 LD and 14:10 LD	0.44 [25]	0.405[30]	21.7 [30]
Saxicola torquata rubicola	9 males	- 30.0 ± 32.7 [9]	1	12.25:11.75	0.48 [26]	0.256[30]	14.9 [30]

				LD			
Sturnus vulgaris	18 males	33.7 ± 74.6 [10]	1	12:12 LD	0.72 [14,16,27]	0.877[30]	82.3 [14]
Sylvia borin	4 males	- 25.7 ± 61.5 [10, 11]	1	12:12 LD	0.46 [16,22]	0.416[30]	19.1 [30]
Sylvia atricapilla	4 males	- 51.7 ± 27.2 [11]	1	12:12 LD	0.41 [16,22]	0.413[30]	18.9 [30]
Calidris canutus	16 unknown	6.8 ± 37.3 [12]	0,1	12:12 LD	0.81 [28]	0.880[32]	130.0 [32]
Calidris tenuirostris	4 unknown	8.7 ± 45.6 [13]	0,1	12:12 LD	0.9 [29]	1.255[33]	149.3 [33]

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