

# Unexpected diversity in socially synchronized rhythms of shorebirds

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The behavioural rhythms of organisms are thought to be under strong selection, influenced by the rhythmicity of the environment<sup>1–4</sup>. Such behavioural rhythms are well studied in isolated individuals under laboratory conditions<sup>1,5</sup>, but free-living individuals have to temporally synchronize their activities with those of others, including potential mates, competitors, prey and predators<sup>6–10</sup>. Individuals can temporally segregate their daily activities (for example, prey avoiding predators, subordinates avoiding dominants) or synchronize their activities (for example, group foraging, communal defence, pairs reproducing or caring for offspring)<sup>6–9,11</sup>. The behavioural rhythms that emerge from such social synchronization and the underlying evolutionary and ecological drivers that shape them remain poorly understood<sup>5–7,9</sup>. Here we investigate these rhythms in the context of biparental care, a particularly sensitive phase of social synchronization<sup>12</sup> where pair members potentially compromise their individual rhythms. Using data from 729 nests of 91 populations of 32 biparentally incubating shorebird species, where parents synchronize to achieve continuous coverage of developing eggs, we report remarkable within- and between-species diversity in incubation rhythms. Between species, the median length of one parent's incubation bout varied from 1–19 h, whereas period length—the time in which a parent's probability to incubate cycles once between its highest and lowest value—varied from 6–43 h. The length of incubation bouts was unrelated to variables reflecting energetic demands, but species relying on crypsis (the ability to avoid detection by other animals) had longer incubation bouts than those that are readily visible or who actively protect their nest against predators. Rhythms entrainable to the 24-h light–dark cycle were less prevalent at high latitudes and absent in 18 species. Our results indicate that even under similar environmental conditions and despite 24-h environmental cues, social synchronization can generate far more diverse behavioural rhythms than expected from studies of individuals in captivity<sup>5–7,9</sup>. The risk of predation, not the risk of starvation, may be a key factor underlying the diversity in these rhythms.

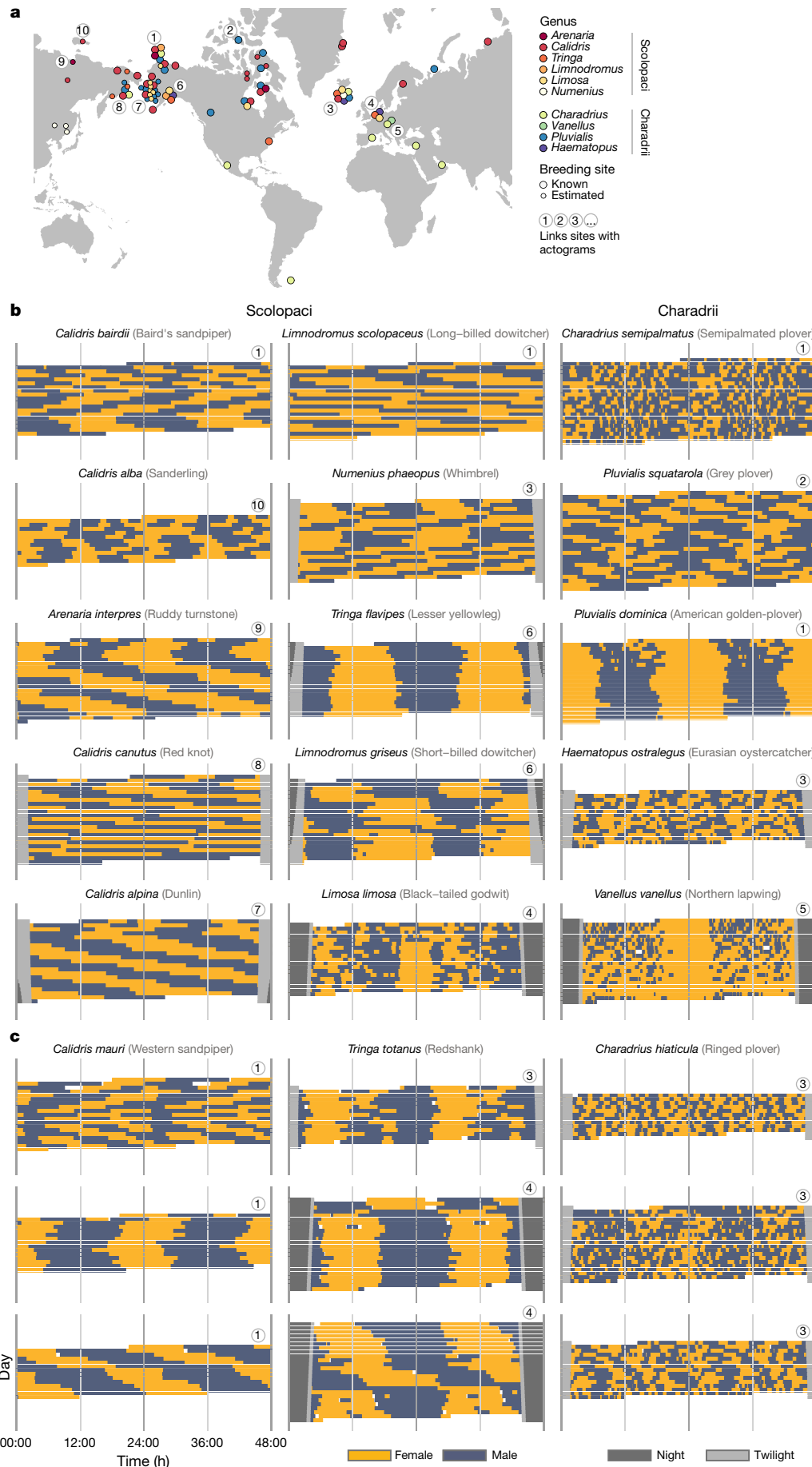
Incubation by both parents prevails in almost 80% of non-passerine families<sup>13</sup> and is the most common form of care in shorebirds<sup>14</sup>. Biparental shorebirds are typically monogamous<sup>15</sup>, most species lay three or four eggs in an open nest on the ground<sup>15</sup> and cover their eggs almost continuously<sup>13</sup>. Pairs achieve this through synchronization of

their activities so that one of them is responsible for the nest at a given time (an incubation bout). Alternating female and male bouts generate an incubation rhythm with a specific period length (cycle of high and low probability for a parent to incubate).

We used diverse monitoring systems (Methods and Extended Data Table 1) to collect data on incubation rhythms from 91 populations of 32 shorebird species belonging to 10 genera (Fig. 1a), extracted the length of 34,225 incubation bouts from 729 nests and determined the period length for pairs in 584 nests (see Methods, Extended Data Figs 1, 2).

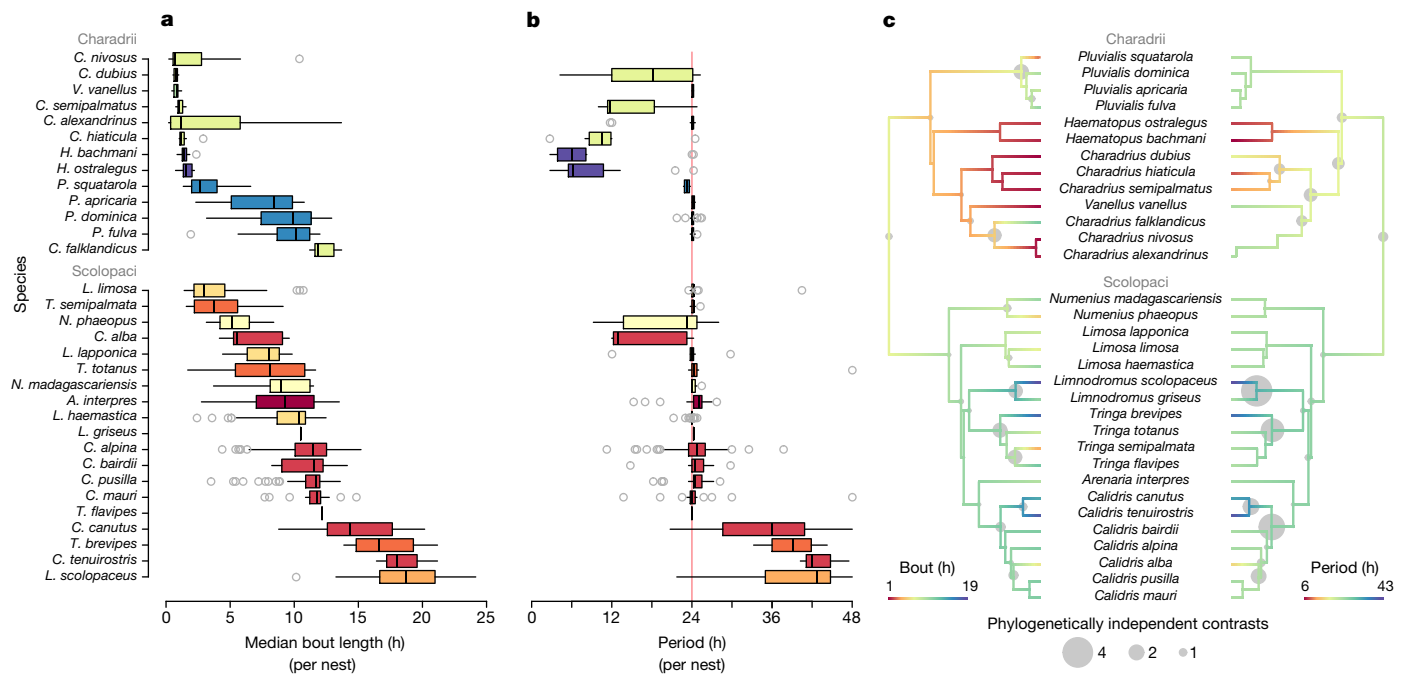
We found vast between- and within-species variation in incubation bout length and in period length (Figs 1–3 and Extended Data Fig. 3). Different species, but also different pairs of the same species, adopted notably different incubation rhythms, even when breeding in the same area (see, for example, incubation rhythms in Barrow, Alaska, represented by '1' in Fig. 1b, c; incubation rhythms for each nest can be found in the supplementary actograms of ref. 16). In some pairs, parents exchanged incubation duties about 20 times a day (Fig. 2a; for example *Charadrius semipalmatus*, Fig. 1b), whereas in others a single parent regularly incubated for 24 h (Fig. 2a; for example *Limnodromus scolopaceus*, Fig. 1b), with exceptional bouts of up to 50 h (supplementary actograms of ref. 16). Similarly, incubation rhythms of pairs in 22% of nests followed a strict 24-h period (Fig. 2b; for example *Tringa flavipes*, Fig. 1b), whereas the rhythms of others deviated markedly from a 24-h period (Fig. 2b) resulting in ultradian (<20 h in 12% of nests; for example *Numenius phaeopus*; Fig. 1b), free-running-like (for example *Calidris alpina*; Fig. 1b) and infradian rhythms (>28 h in 8% of nests), with some having period lengths up to 48 h (for example *Limnodromus scolopaceus*; Fig. 1b). This variation in period length partly related to the variation in bout length (Fig. 3). In the suborder Scolopaci, period length correlated positively with median bout length, but in the suborder Charadrii species with 24-h periods had various bout lengths, and species with similar bout lengths had different period lengths.

Despite substantial within-species variation, we found a strong evolutionary signal for both bout and period length with a coefficient of phylogenetic signal  $\lambda$  close to 1 (Extended Data Table 2). This is consistent with the notion that biological rhythms are largely genetically determined and conserved among related species<sup>8–10</sup>. However, the phylogenetic effect seems unevenly distributed over the taxonomic level. Suborder explained 33% of the phenotypic variance in both bout



**Figure 1 | Map of studied breeding sites and the diversity of shorebird incubation rhythms.** **a**, Map of breeding sites with data on incubation rhythms. The colour of the dots indicates the genus (data from multiple species per genus may be available), the size of the dots refers to data quality (large dots, exact breeding site known; small dots, breeding site estimated, see Methods). For nearby or overlapping locations, the dots are scattered to increase visibility. Contours of the map were made with Natural Earth, <http://www.naturalearthdata.com>.

**b, c**, Illustrations of between-species diversity (**b**) and within-species diversity (**c**; note that the three rhythms for *Calidris mauri* and *Calidris hiaticula* come from the same breeding location). Each actogram depicts the bouts of female (yellow) and male (blue) incubation at a single nest over a 24-h period, plotted twice, so that each row represents two consecutive days. If present, twilight is indicated by light grey bars and corresponds to the time when the sun is between  $6^\circ$  and  $0^\circ$  below the horizon, night is indicated by dark grey bars and corresponds to the time when the sun is  $>6^\circ$  below the horizon. Twilight and night are omitted in the centre of the actogram (24:00) to make the incubation rhythm visible. The circled numbers (1–10) indicate the breeding site of each pair and correspond to the circled numbers on the map in **a**.



**Figure 2 | Variation in incubation rhythms and its estimated evolution.** **a, b**, Box plots are ordered by species (within suborder) from the shortest to the longest median bout length, and depict the genus (colour as in Fig. 1a), median (vertical line inside the box), 25–75th percentiles (box) 25th and 75th percentiles minus or plus  $1.5 \times$  interquartile range, respectively, or the minimum and maximum value, whichever is smaller (box) outliers (circles).  $n_{\text{median bout length}} = 729$  and  $n_{\text{period}} = 584$

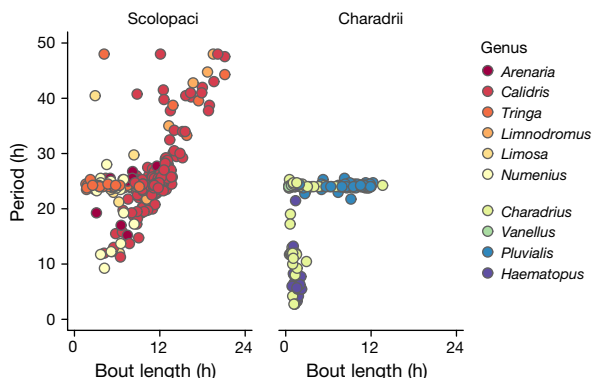
and period length, with the Scolopaci having longer incubation bouts and periods than the Charadrii (Extended Data Table 3 and Figs 2, 3). Species explained 41% of the phenotypic variation in bout length and 46% in period length, but genus explained little ( $<1\%$  in both bout and period length; Extended Data Table 3), suggesting that despite a strong phylogenetic signal, these traits can rapidly diverge (Fig. 2c).

Two ecological factors may explain the observed variation in bout length. First, the ‘energetic demands hypothesis’ stipulates that the length of an incubation bout depends on the energetic state of the bird<sup>13,17</sup>. This predicts that large species will have longer incubation bouts than smaller species, because they radiate less body heat per unit of mass and that incubation bouts will shorten with increasing breeding latitude, because—everything else being equal—energy

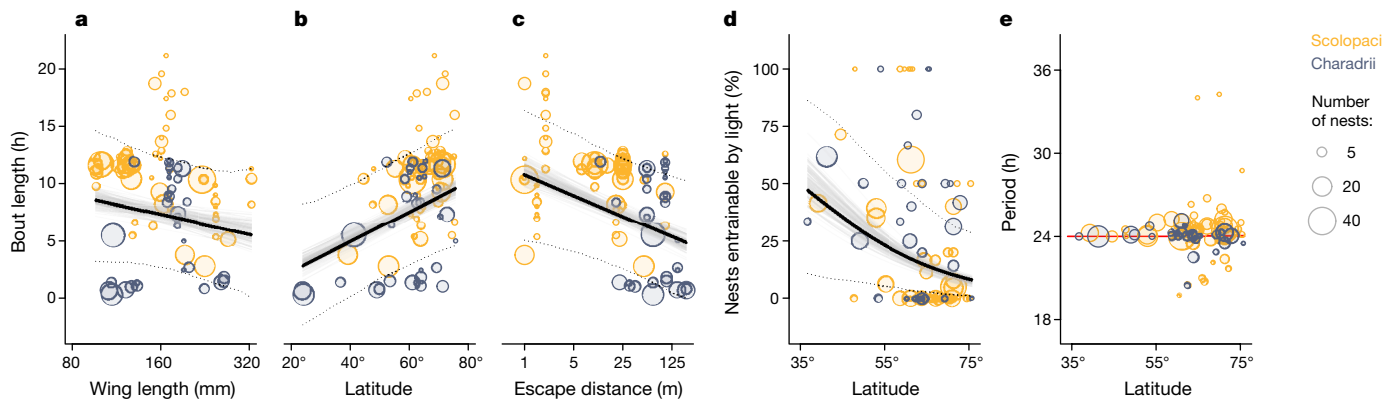
stores will deplete faster in colder environments (Extended Data Fig. 4a, b shows latitudinal cline in summer temperatures). However, bout length was unrelated to body size (Fig. 4a) and correlated positively (instead of negatively) with latitude (Fig. 4b). These correlational results across populations and species support recent experimental findings within species<sup>18</sup> and suggest that in biparentally incubating shorebirds energetic demands are not an important ecological driver underlying variation in bout length.

An alternative explanation for variation in the length of incubation bouts relates to anti-predation strategies. Those species that rely primarily on parental crypsis (Extended Data Fig. 5a) benefit from reduced activity near the nest, because such activity can reveal the location of the nest to potential predators<sup>19,20</sup>. Thus, in these species, selection will favour fewer change-overs at the nest and therefore longer incubation bouts. By contrast, species that are clearly visible when sitting on the nest or that rely on active anti-predation behaviour (Extended Data Fig. 5b), including having a partner on the watch for predators, leaving the nest long before the predator is nearby and attacking or distracting the predator<sup>15</sup>, obtain no advantage from minimizing activity. For these species, bout length can shorten, which may be advantageous for other reasons (for example, reduced need to store fat). We quantified anti-predation strategy as the distance at which the incubating parent left the nest when approached by a human (escape distance), because cryptic species stay on the nest longer (often until nearly stepped upon)<sup>15</sup>. Despite the large geographical distribution of the studied species, with related variability in the suite of predators and predation pressure<sup>21</sup>, and even when controlling for phylogeny (which captures much of the variation in anti-predation strategy, Extended Data Fig. 6), escape distance negatively correlated with the length of incubation bouts (Fig. 4c). This result suggests that bout length co-evolved with the anti-predation strategy.

Under natural conditions, most organisms show 24-h rhythmicity, but during the summer, when most shorebirds breed, the 24-h variation in light decreases with latitude leading to continuous polar daylight



**Figure 3 | Relationship between bout and period length.** Each dot represents a single nest ( $n = 584$  nests), colours depict the genus. In the suborder Scolopaci the median bout length and period length correlate positively ( $r_{\text{Spearman}} = 0.56$ ,  $n = 424$  nests); in the suborder Charadrii, periods longer than approximately 24 h are absent, and there is no simple relationship between bout and period length ( $n = 160$  nests). For species-specific relationships see Extended Data Fig. 3.



**Figure 4 | Predictors of variation in incubation rhythms.**

**a–c**, Relationships between bout length and body size, measured as female wing length (**a**), breeding latitude (**b**) and anti-predation strategy, quantified as escape distance (**c**) for  $n = 729$  nests from 91 populations belonging to 32 species. **d**, The relationship between the proportion of nests with a period length that is entrainable by the 24-h light–dark cycle (that is, period lengths: 3, 6, 12, 24, or 48 h) and breeding latitude ( $n = 584$  nests from 88 populations belonging to 30 species). **e**, The distribution of period length over latitude. The period was standardized to 24 h so that all 24-h harmonics are depicted as 24 h (red line) and respective deviations from each harmonic as deviations from 24 h (for example, a period of 12.5 h is depicted as 25 h). **a–e**, Each circle represents the population

in the northern-most breeding grounds<sup>22</sup> (Extended Data Fig. 4c, d). Such reduced variation in 24-h light intensity may cause a loss of 24-h rhythmicity<sup>23–25</sup>. As a consequence, circadian behavioural rhythms should exhibit a latitudinal cline<sup>22</sup>. As predicted, incubation rhythms with periods that do not follow the 24-h light–dark cycle, such as free-running-like patterns (left column in Fig. 1b), occurred more often in shorebirds breeding at higher latitudes (Fig. 4d). The absolute deviations of periods from 24 h and 24-h harmonics also increased with latitude (Fig. 4e and Extended Data Table 4). Although this supports the existence of a latitudinal cline in socially emerged behavioural rhythms<sup>22</sup>, we found a substantial number of rhythms that defy the 24-h day even at low and middle latitudes (Fig. 4d–e).

Many shorebirds predominantly use tidal habitats, at least away from their breeding ground<sup>15</sup>. To anticipate tidal foraging opportunities, these species may have activity patterns with a period length resembling the tidal period. Because changing to a different rhythm is costly<sup>26</sup>, these tidal activity patterns might carry over to incubation. Although half of our species are tidal away from their breeding grounds, and some forage in tidal areas also during breeding (approximately 12% of populations), in only 5% of nests did pairs display a period length that can be entrained by the tide. Moreover, tidal species had period lengths similar to, not longer than, non-tidal ones (Extended Data Table 4). Hence, unlike the 24-h light–dark cycle, tidal life-history seems to play at best a negligible role in determining incubation rhythms.

Three main questions arise from our results. First, is variation in incubation bout length in cryptic species related to the actual predation pressure? This can be tested by comparing bout length between populations of a particular species that are exposed to different predator densities, or between years that differ in predation pressure. Second, it remains unclear how the diverse social rhythms emerge. Are these rhythms a consequence of behavioural flexibility, or a ‘fixed’ outcome of synchronization between the circadian clocks of the two individuals involved? An experimental study on ring doves (*Streptopelia risoria*) suggests that parents may even use two timers—circadian oscillation and interval timing—to determine when to incubate<sup>27</sup>. Parents rapidly adjusted their schedules to phase-shifted photoperiods and their incubation rhythm ‘ran free’ in constant dim illumination (implying a circadian mechanism), whereas an experimental delay in the onset of an incubation bout did not change the length of the bout because the incubating parent refused to leave the nest until its incubation bout reached the ‘typical’ duration

(implying interval timing). Third, what are the fitness consequences for the parents of having a certain incubation rhythm? For example, the costs of having a particular incubation rhythm may be unevenly distributed between the two parents (for instance, because one parent is on incubation duty when food is more readily available, or because one parent ‘enforces’ its own rhythm at a cost to the other parent). In conclusion, our results reveal that under natural conditions social synchronization can generate much more diverse rhythms than expected from previous work<sup>5–7,9,28</sup>, and that these rhythms often defy the assumption of entrainment to the 24-h day–night cycle. Risk of predation, rather than risk of starvation, seems to have a key role in determining some of the variation in incubation rhythms. We describe this diversity in the context of biparental incubation, but diverse behavioural rhythms may also arise in many other social settings (for example, in the context of mating interactions<sup>25</sup> or vigilance behaviour during group foraging). Essentially, the reported diversity suggests that the expectation that individuals within a pair (or group) should optimize their behavioural rhythms relative to the 24-h day may be too simplistic, encouraging further study of the evolutionary ecology of plasticity in circadian clocks.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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## METHODS

**Recording incubation.** Incubation data were obtained between 1994 and 2015, for as many shorebird species ( $n = 32$ ) and populations ( $n = 91$ ) as possible (that is, no statistical methods were used to predetermine sample size), using six methods (for specifications of the equipment see Extended Data Table 1). (1) In 261 nests, a radio frequency identification reader (RFID) registered the presence of tagged parents at the nest. The passive integrated tag was either embedded in a plastic flag<sup>31,32</sup>, with which the parents were banded, or glued to the tail feathers<sup>33</sup>. In 200 nests the RFID was combined with a temperature probe placed between the eggs. The temperature recordings allowed us to identify whether a bird was incubating even in the absence of RFID readings; an abrupt change in temperature marked the start or end of incubation<sup>31</sup>. (2) For 396 nests, light-loggers were mounted to the plastic flag or a band that was attached to the bird's leg<sup>34,35</sup>. The logger recorded maximum light intensity (absolute or relative) for a fixed sampling interval (2–10 min). An abrupt change in light intensity (as opposed to a gradual change caused, for example, by twilight) followed by a period of low or high light intensity marked the start or end of the incubation period (Extended Data Fig. 2). (3) For nine nests a GPS tag, mounted on the back of the bird, recorded the position of the bird<sup>36</sup>. The precision of the position depends on cloud cover and sampling interval<sup>36</sup>. Hence, to account for the imprecision in GPS positions, we assumed incubation whenever the bird was within 25 m of the nest (Extended Data Fig. 2b). (4) At three nests automated receivers recorded signal strength of a radio tag attached to the rump of a bird; whenever a bird incubated, the strength of the signal remained constant<sup>24</sup> (supplementary actograms; pages 257–259 of ref. 16). (5) At 53 nests video cameras were used to identify the incubating parents. (6) Eight nests were continuously observed. In (5) and (6) parent identification was based on plumage, colour rings or radio tag. In one of the populations, three different methods were used, in seven populations representing seven species two methods were used. In one nest, two methods were used simultaneously (Extended Data Fig. 2b).

**Extraction of incubation bouts.** An incubation bout was defined as the total time allocated to a single parent (that is, the time between the arrival of a parent at and its departure from the nest followed by incubation of its partner). Bout lengths were only extracted if at least 24 h of continuous recording was available for a nest; in such cases, all bout lengths were extracted. For each nest, we transformed the incubation records to local time as UTC time + (longitude of the nest/15). Incubation bouts from RFIDs, videos and continuous observations were mostly extracted by an R script and the results verified by visualizing the extracted and the raw data<sup>16,31,37,38</sup>; otherwise, M.B. extracted the bouts manually from plots of raw data<sup>39,40</sup> (plots of raw data and extracted bouts for all nests are in the supplementary actograms of ref. 16; the actograms were generated by the ggplot and xyplot functions from the ggplot2 and lattice R-packages<sup>41–43</sup>). Whenever the start or end of a bout was unclear, we classified these bouts as uncertain (see next paragraph for treatment of uncertain bouts). In case of light-logger data, the light recordings before and after the breeding period, when the birds were definitely not incubating, helped to distinguish incubation from non-incubation. Whenever an individual tagged with a light-logger nested in an environment where the sun was more than 6° below the horizon for part of a day (that is, night), we assumed an incubation bout when the individual started incubating before the night started and ended incubating after the night ended. When different individuals incubated at the beginning versus at the end of the night, we either did not quantify these bouts or we indicated the possible time of exchange (based on trends in previous exchanges), but classified these bouts as uncertain (see supplementary actograms<sup>16</sup>). In total, we extracted 34,225 incubation bouts.

The proportion of uncertain bouts within nests had a distribution skewed towards zero (median = 0%, range, 0–100%,  $n = 729$  nests), and so did the median proportion of uncertain bouts within populations (median = 2%, range, 0–74%,  $n = 91$  populations). Excluding the uncertain bouts did not change our estimates of median bout length (Pearson's correlation coefficient for median bout length based on all bouts and without uncertain bouts:  $r = 0.96$ ,  $n = 335$  nests with both certain and uncertain bouts). Hence, in further analyses all bouts were used to estimate median bout length.

Note that in some species sexes consistently differed in bout length (Fig. 1b, for example, *Vanellus vanellus*). As these differences are small compared to the between-species differences and because in 27 nests (of 8 species) the sex of the parents was unknown, we used median bout length independent of sex in this study.

**Extraction of period length.** The method used for extracting the period length of incubation rhythm for each nest is described in the Extended Data Fig. 1.

**Extraction of entrainable periods.** We classified 24-h periods and periods with 24-h harmonics (that is, 3, 6, 12, 48 h) as strictly entrainable by 24-h light fluctuations ( $n = 142$  nests out of 584). Including nearest adjacent periods ( $\pm 0.25$  h) increased the number of nests with entrainable periods ( $n = 277$ ), but results of statistical analyses remained quantitatively similar. We consider periods and

harmonics of 12.42 h (that is, 3.1, 6.21, 12.42, 24.84 h) as strictly entrainable by tide. However, because the periods in our data were extracted in 0.25-h intervals (Extended Data Fig. 1), we classified periods of 3, 6.25, 12.5, 24.75 h (that is, those closest to the strict tide harmonics) as entrainable by tide ( $n = 32$  nests out of 584). Including also the second nearest periods (that is, 3.25, 6, 12.25, 25) increased the number of nests entrainable by tide to  $n = 55$ .

**Population or species life-history traits.** For 643 nests, the exact breeding location was known (nests or individuals were monitored at the breeding area). For the remaining 86 nests (from 27 populations representing 8 species, where individuals were tagged with light-loggers at the wintering area), the breeding location was roughly estimated from the recorded 24-h variation in daylight, estimated migration tracks, and the known breeding range of the species<sup>44–51</sup>. One exact breeding location was in the Southern Hemisphere, so we used absolute latitude in analyses. Analyses without populations with estimated breeding-location or without the Southern Hemisphere population generated quantitatively similar estimates as the analyses on full data.

For each population, body size was defined as mean female wing length<sup>52</sup>, either for individuals measured at the breeding area or at the wintering area. In case no individuals were measured, we used the mean value from the literature (see open access data for specific values and references<sup>53</sup>).

Anti-predation strategy was assessed by estimating the escape distance of the incubating bird when a human approached the nest, because species that are cryptic typically stay on the nest much longer than non-cryptic species, sometimes until nearly stepped upon<sup>48,54</sup>. Escape distance was obtained for all species. Forty-four authors of this paper estimated the distance (in metres) for one or more species based on their own data or experience. For ten species, we also obtained estimates from the literature<sup>48</sup>. We then used the median 'estimated escape distance' for each species. In addition, for 13 species we obtained 'true escape distance'. Here, the researcher approached a nest (of known position) and either estimated his distance to the nest or marked his position with GPS when the incubating individual left the nest. For each GPS position, we calculated the Euclidian distance from the nest. In this way we obtained multiple observations per nest and species, and we used the median value per species (weighted by the number of estimates per nest) as the true escape distance. The species' median estimated escape distance was a good predictor of the true escape distance (Pearson's correlation coefficient:  $r = 0.89$ ,  $n = 13$  species). For analysis, we defined the escape distance of a species as the median of all available estimates.

For each species, we determined whether it predominantly uses a tidal environment outside its breeding ground, that is, has tidal versus non-tidal life history (based on refs 48, 50, 51). For each population with exact breeding location, we scored whether tidal foraging habitats were used by breeding birds for foraging (for three populations this information was unknown)<sup>53</sup>. For all populations with estimated breeding location we assumed, based on the estimated location and known behaviour at the breeding grounds, no use of tidal habitat.

**Statistical analyses.** Unless specified otherwise, all analyses were performed on the nest level using median bout length and extracted period length.

We used phylogenetically informed comparative analyses to assess how evolutionary history constrains the incubation rhythms (estimated by Pagel's  $\lambda$  coefficient of phylogenetic signal<sup>55,56</sup>) and to control for potential non-independence among species due to common ancestry. This method explicitly models how the covariance between species declines as they become more distantly related<sup>55,57,58</sup>. We used the Hackett<sup>59</sup> backbone phylogenetic trees available at <http://birdtree.org> (ref. 60), which included all but one species (*Charadrius nivosus*) from our dataset. Following a subsequent taxonomic split<sup>61</sup>, we added *C. nivosus* to these trees as a sister taxon of *C. alexandrinus*. Phylogenetic uncertainty was accounted for by fitting each model with 100 phylogenetic trees randomly sampled from 10,000 phylogenies at <http://birdtree.org> (ref. 60).

The analyses were performed with Bayesian phylogenetic mixed-effect models (Fig. 4 and Extended Data Tables 2, 4) and the models were run with the MCMCglmm function from the R package MCMCglmm<sup>62</sup>. In all models, we also accounted for multiple sampling within species and breeding site (included as random effects). In models with a Gaussian response variable, an inverse-gamma prior with shape and scale equal to 0.001 was used for the residual variance (that is, variance set to 1 and the degree of belief parameter to 0.002). In models with binary response variables, the residual variance was fixed to 1. For all other variance components the parameter-expanded priors were used to give scaled  $F$ -distributions with numerator and denominator degrees of freedom set to 1 and a scale parameter of 1,000. Model outcomes were insensitive to prior parameterization. The MCMC chains ran for 2,753,000 iterations with a burn-in of 3,000 and a thinning interval of 2,500. Each model generated approximately 1,100 independent samples of model parameters (Extended Data Tables 2, 4). Independence of samples in the Markov chain was assessed by tests for autocorrelation between samples and by using graphic diagnostics.

First, we used MCMCglmm to estimate Pagel's  $\lambda$  (phylogenetic signal) for bout and period length (Gaussian), and to show that our estimates of these two incubation variables were independent of how often the incubation behaviour was sampled ('sampling' in min, ln-transformed; Extended Data Table 2). Hence, in subsequent models, sampling was not included.

Then, we used MCMCglmm to model variation in bout length and period length (Extended Data Table 4). Bout length was modelled as a continuous response variable and latitude (in degrees, absolute), female wing length (mm, ln-transformed) and approach distance (m, ln-transformed) as continuous predictors. Predictors had low collinearity (at nest, population and species level; all Pearson or Spearman correlation coefficients  $|r| < 0.28$ ). To test for potential entrainment to 24-h, period length was modelled as a binary response variable (1 = rhythms with period of 3, 6, 12, 24, or 48 h; 0 = rhythms with other periods) and latitude as a continuous predictor. To test how circadian period varies with latitude or life history, the period was transformed to deviations from 24 h and 24-h harmonics and scaled by the time span between the closest harmonic and the closest midpoint between two harmonics. For example, a 42-h period deviates by -6 h from 48 h (the closest 24-h harmonic) and hence -6 h was divided by 12 h (the time between 36 h—the midpoint of two harmonics—and 48 h—the closest harmonic). This way the deviations spanned from -1 to 1 with 0 representing 24 h and its harmonics. The absolute deviations were then modelled as a continuous response variable and latitude as continuous predictor. The deviations were also modelled as a continuous response and species life history (tidal or not) as categorical predictor.

In all models the continuous predictor variables were centred and standardized to a mean of zero and a standard deviation of one.

We report model estimates for fixed and random effects, as well as for Pagel's  $\lambda$ , by the modes and the uncertainty of the estimates by the highest posterior density intervals (referred to as 95% CI) from the joint posterior distributions of all samples from the 100 separate runs, each with 1 of the 100 separate phylogenetic trees from <http://birdtree.org> (ref. 60).

To help interpret the investigated relationships we assessed whether incubation rhythms evolved within diverged groups of species by plotting the evolutionary tree of the incubation rhythm variables (Fig. 2c), as well as of the predictors (Extended Data Fig. 6).

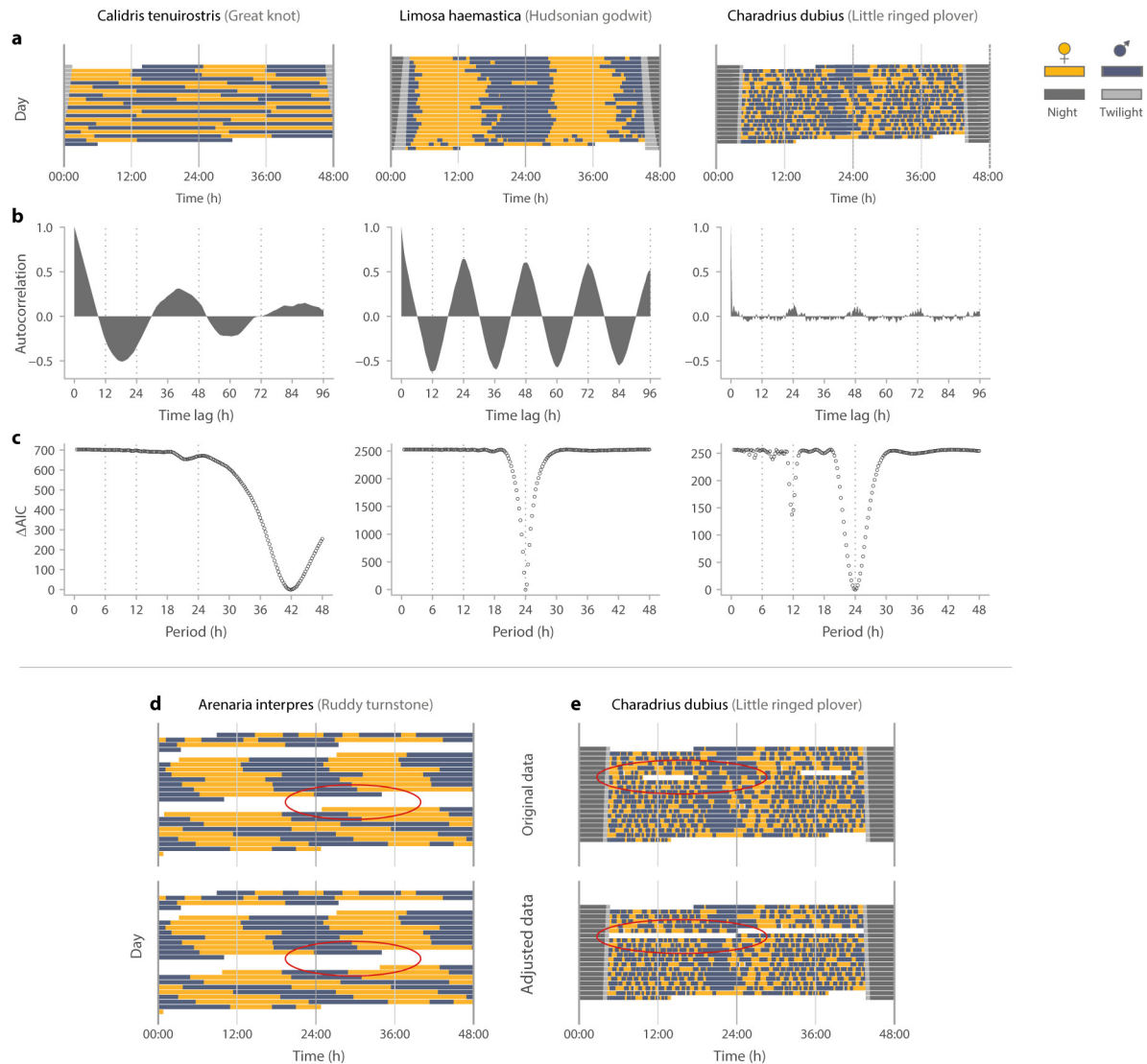
The source of phylogenetic constraint in bout and period length was investigated by estimating the proportion of phenotypic variance explained by suborder, genus and species (Extended Data Table 3). The respective mixed models were also specified with MCMCglmm<sup>62</sup> using the same specifications as in the phylogenetic models. Because suborder contained only two levels, we first fitted an intercept mixed model with genus, species, and breeding site as random factors, and used it to estimate the overall phenotypic variance. We then entered suborder as a fixed factor and estimated the variance explained by suborder as the difference between the total variance from the first and the second model. To evaluate the proportion of the variance explained by species, genus and breeding site, we used the estimates from the model that included suborder.

R version 3.1.1 (ref. 63) was used for all statistical analyses.

**Code availability.** All statistical analyses, figures, and the supplementary actograms are replicable with the open access information, including computer software and code for R, available at the Open Science Framework, <https://osf.io/wxufm/> (ref. 16).

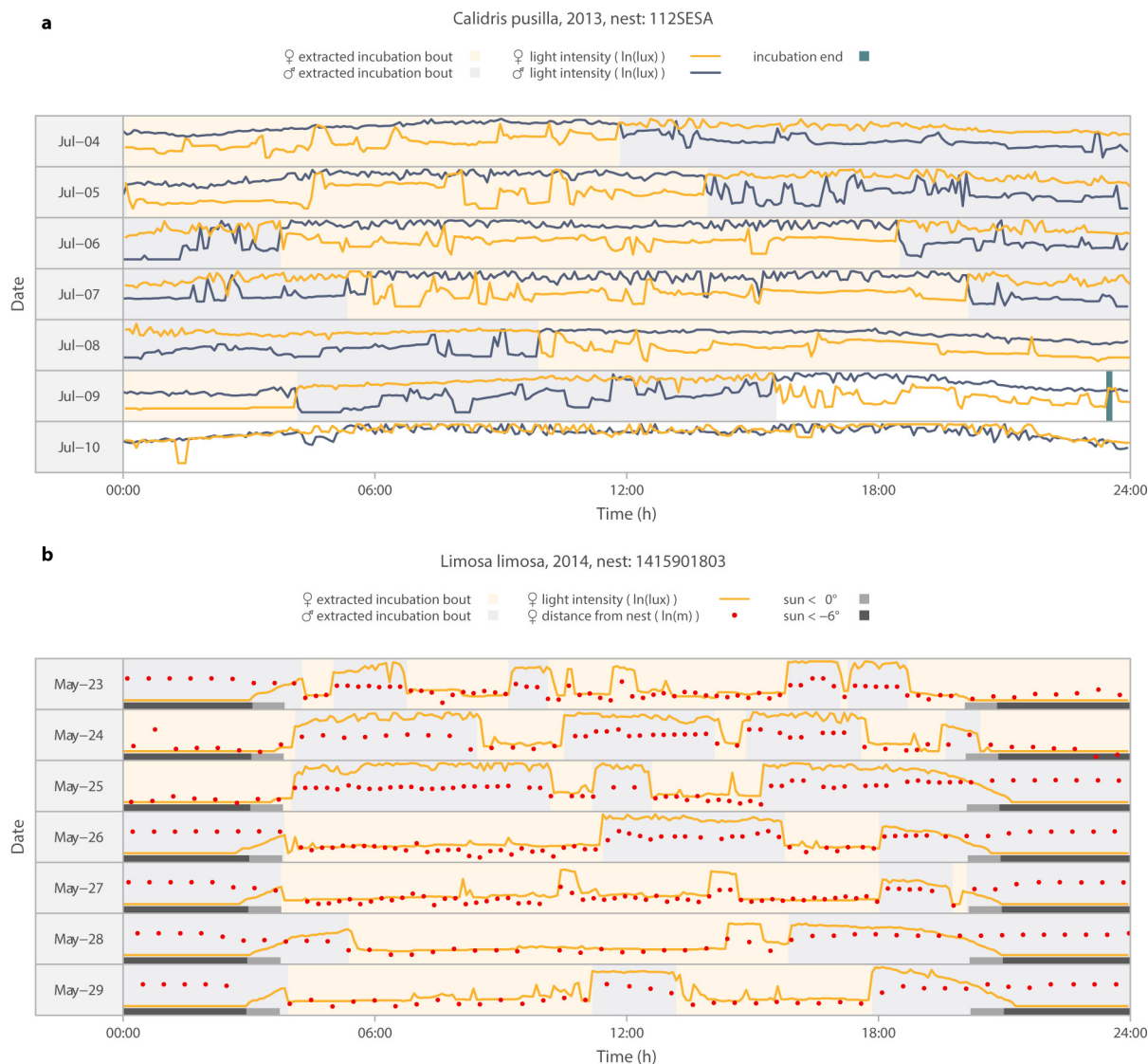
**Data availability.** Primary and extracted data that support the findings of this study are freely available from the Open Science Framework, <https://osf.io/wxufm/> (ref. 16). Source data for Figs 1–4 are provided with the paper.

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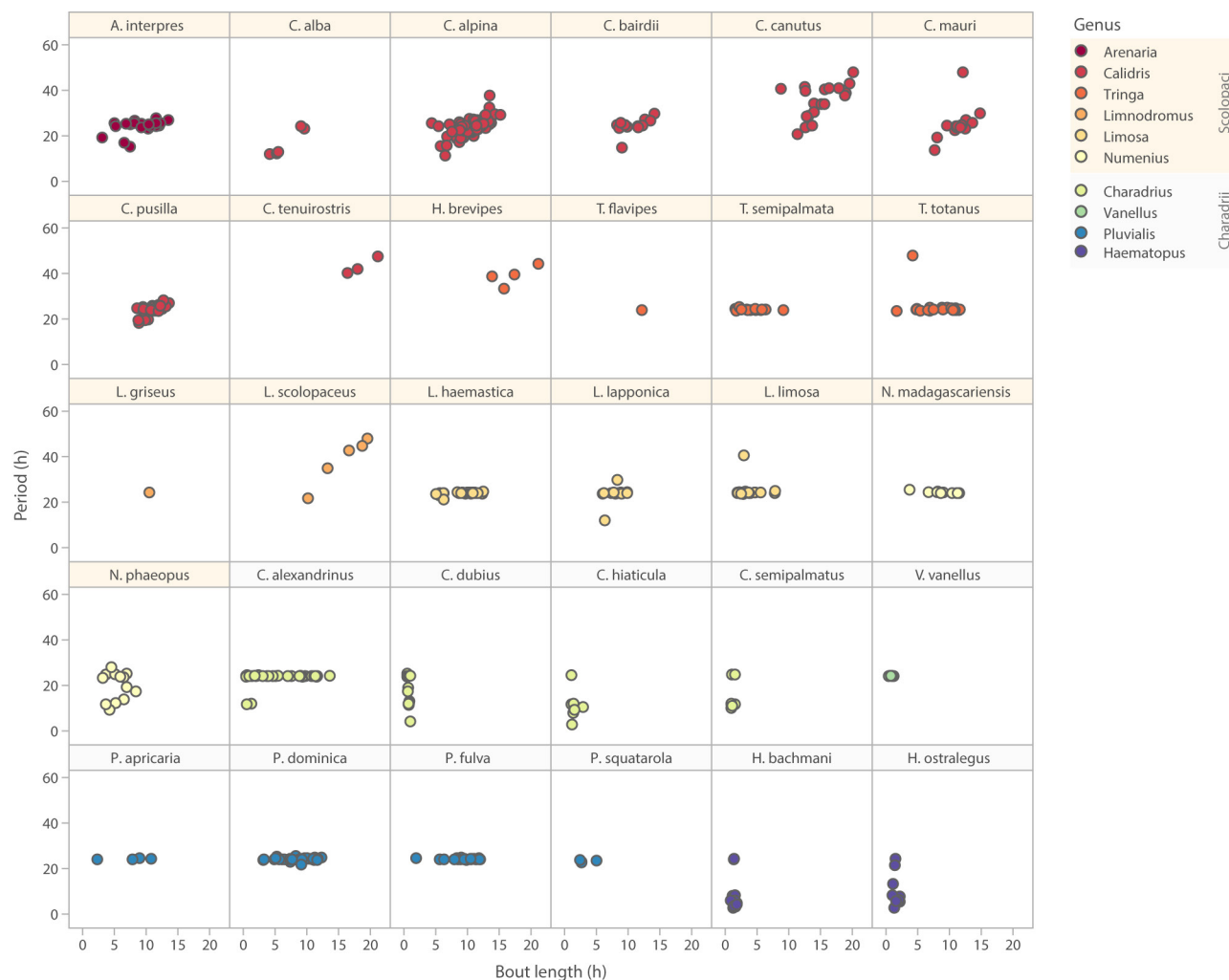
**Extended Data Figure 1 | Extracting period length of incubation rhythms.** **a–c**, Each column represents an example for a specific nest with long, intermediate and short incubation bouts. **a**, From the extracted bout lengths we created a time series that indicated—for each nest and for every 10 min interval—whether a specific parent (female, if sex was known) incubated or not. Exchange gaps (no parent on the nest) had to be  $<6$  h to be included (for treatment of exchange gaps  $>6$  h see **d**, **e**). **b**, We then estimated the autocorrelation for each 10-min time-lag up to 4 days (R ‘acf’ function<sup>63</sup>). Positive values indicate a high probability that the female was incubating, negative values indicate that it was more likely that the male was incubating. We used only nests that had enough data to estimate the autocorrelation pattern ( $n = 584$  nests from 88 populations of 30 species). The visualized autocorrelation time series never resembled white or random noise indicative of an arrhythmic incubation pattern. To determine the period (that is, cycle of high and low probability for a parent to incubate) that dominated the incubation rhythm, we fitted to the autocorrelation estimates a series of periodic logistic regressions. In each regression, the time lag (in hours) transformed to radians was represented by a sine and cosine function  $f(t) = a_0 + b\left(\cos \frac{2\pi t}{T}\right) + c\left(\sin \frac{2\pi t}{T}\right) + e$ , where  $f(t)$  is the autocorrelation at time-lag  $t$ ;  $a_0$  is the intercept;  $b$  is the

slope for sine and  $c$  the slope for cosine,  $T$  represents the length of the fitted period (in hours), and  $e$  is an error term. We allowed the period length to vary from 0.5 h to 48 h (in 15 min intervals, giving 191 regressions). **c**, By comparing the Akaike’s information criterion<sup>64</sup> (AIC) of all regressions, we estimated, for each nest, the length of the dominant period in the actual incubation data (best fit). Regressions with  $\Delta\text{AIC}$  ( $\text{AIC}_{\text{model}} - \text{AIC}_{\text{min}}$ ) close to 0 are considered as having strong empirical support, while models with  $\Delta\text{AIC}$  values ranging from 4–7 have less support<sup>64</sup>. In 73% of all nests, we determined a single best model with  $\Delta\text{AIC} \leq 3$  (**c**, middle  $\Delta\text{AIC}$  graph), in 20% of nests two best models emerged and in 6% of nests 3 or 4 models had  $\Delta\text{AIC} \leq 3$  (**c**, left and right  $\Delta\text{AIC}$  graphs). However, in all but three nests, the models with the second-, third- and so on best  $\Delta\text{AIC}$  were those with period lengths closest to the period length of the best model (**c**, left and right  $\Delta\text{AIC}$  graphs). This suggests that multiple periodicities are uncommon. **d**, **e**, The extraction of the period length (described in **a–c**) requires continuous data sets, but some nests had long ( $>6$  h) gaps between two consecutive incubation bouts, for example because of equipment failure or because of unusual parental behaviour. In such cases, we excluded the data from the end of the last bout until the same time the following day, if data were then available again (**d**), or we excluded the entire day (**e**).

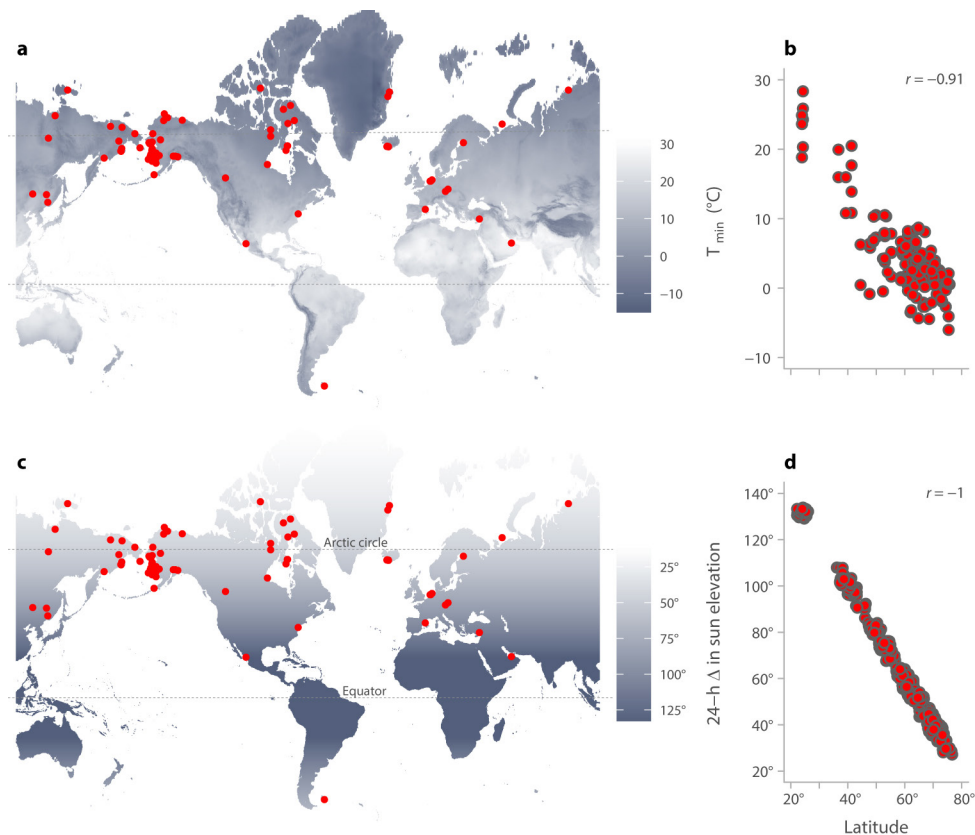


**Extended Data Figure 2 | Extracting incubation bouts from light-logger data.** **a**, An example of a nest with a light intensity signal from both parents (yellow line, female; blue line, male). The incubation bouts for a given parent reflect periods dominated by lower light values compared to those of the partner. Note the sharp drop in the light levels at the beginning of each incubation bout and the sharp increase in the light levels at the end. Change-overs between partners occur when the light signal lines cross. Such pronounced changes in light intensity detected by the logger were used to assign incubation even when only a single parent was tagged. Note that after the chicks hatch and leave the nest (9 July, vertical bar), the light intensity signals from both parents remain similar. **b**, An example

of a nest where one incubating parent was simultaneously equipped with a light-logger and with a GPS tag. The yellow line indicates light levels, red dots indicate the distance of the bird to the nest. As expected, low light levels co-occur with close proximity to the nest, and therefore reflect periods of incubation. Although light levels decrease during twilight (light grey horizontal bar), the recordings were still sensitive enough to reflect periods of incubation, that is, the light signal matches the distance (for example 25 May: female incubated during dawn, but was off the nest during dusk). **a**, **b**, Rectangles in the background indicate incubation bouts (female, light yellow polygon; male, light blue polygon).

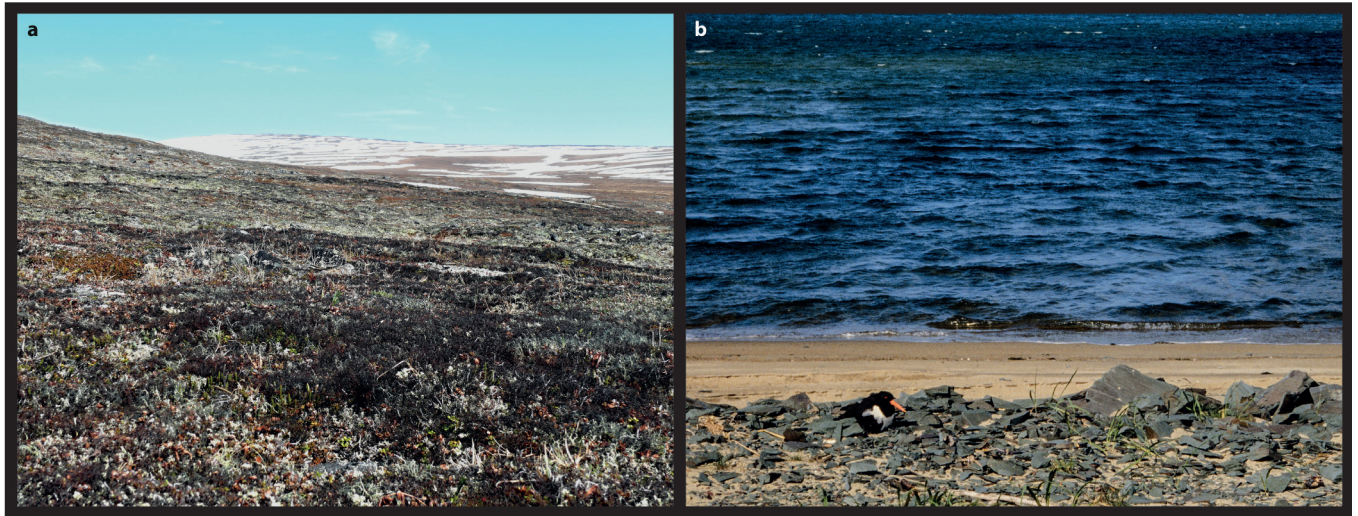


**Extended Data Figure 3 | Relationship between bout and period length for 30 shorebird species.** Each dot represents one nest ( $n = 584$  nests), colours indicate the genus.



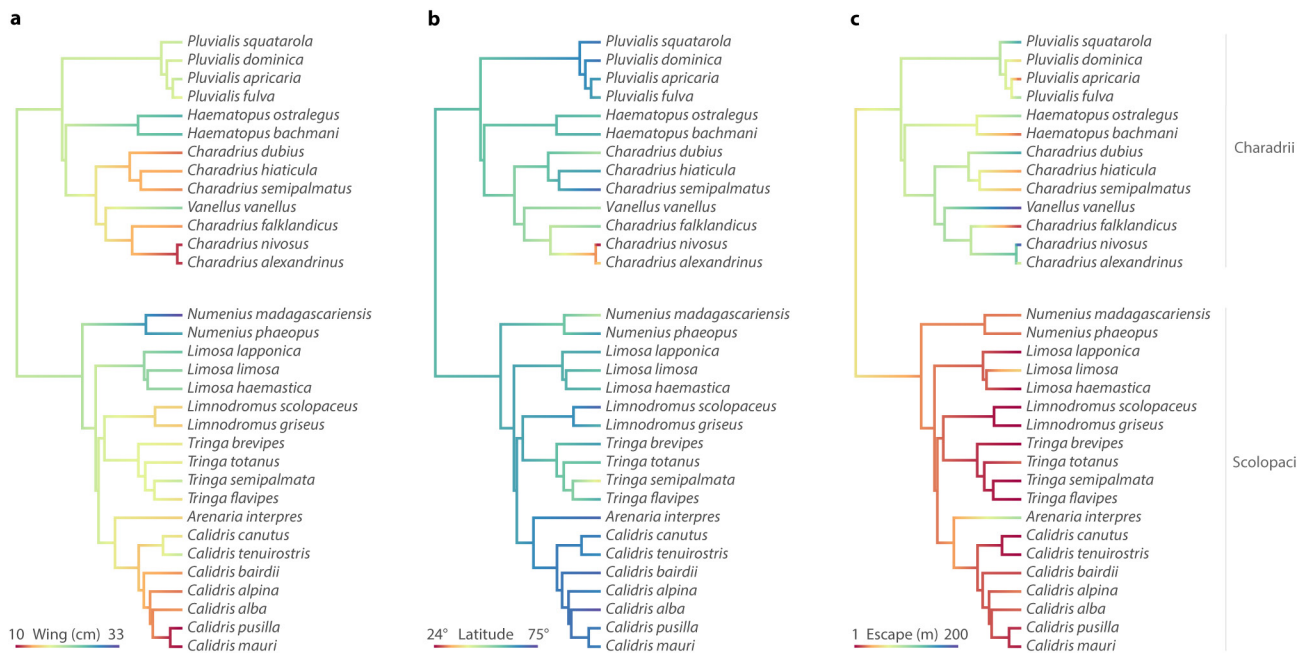
**Extended Data Figure 4 | Ecological correlates of latitude.** **a**, Variation in minimum temperature across the globe represented by mean minimum June temperature for the Northern Hemisphere and mean minimum December temperature for the Southern Hemisphere. **b**, Correlation between absolute latitude and the mean minimum temperature of the month ( $n = 729$  nests). For each nest we used the month that contained most of the incubation data. For maximum temperature the correlation was the same ( $r = -0.91$ ,  $n = 729$  nests). **c**, Daily variation in sun elevation (that is, in light conditions) are represented as the difference between the

noon and midnight sun elevation for the summer solstice in the Northern Hemisphere and the winter solstice in the Southern Hemisphere. **d**, Correlation between absolute latitude and daily variation in sun elevation for mid-day of incubation data for each nest ( $n = 729$  nests). The points are jittered, as otherwise they form a straight line. **a**, **c**, Red points indicate the breeding site for each population ( $n = 91$ ). **a**, **b**, The minimum and maximum monthly temperature data were obtained from <http://www.worldclim.org> using the raster R-package<sup>65</sup>. **c**, **d**, Sun-elevation was obtained by the 'solarpos' function from the maptools R-package<sup>66</sup>.



**Extended Data Figure 5 | Between-species variation in parental crypsis during incubation.** **a, b,** Shorebirds vary in how visible they are on the nest while incubating. The nearly invisible great knot (*Calidris tenuirostris*; **a**; central and facing right) sits tight on the nest when approached by a

human until nearly stepped upon. In contrast, the conspicuous Eurasian oystercatcher (*Haematopus ostralegus*; **b**) is visible on the nest from afar and when approached by a human leaves the nest about 100 m in advance (Credits: **a**, M. Šálek; **b**, J. van de Kam).



**Extended Data Figure 6 | Phylogenetic relationships for predictors.** **a**, Body size, estimated as female wing length. **b**, Latitude (absolute). **c**, Escape distance. **a–c**, We visualized the evolution of these traits<sup>29,67</sup> using the median (**a**, **b**; based on population medians), estimates of escape distance for each species (**c**) and one of the 100 sampled trees (see Methods).

Extended Data Table 1 | Incubation monitoring methods and systems

| Method                                           | Model                                                                                | Company                                                    | www                                                                                                                                                                           | Year      | Sampling interval (min) | <i>n</i> populations | <i>n</i> nests | <i>n</i> both parents tagged |
|--------------------------------------------------|--------------------------------------------------------------------------------------|------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|-------------------------|----------------------|----------------|------------------------------|
| RFID + tag embedded in the flag <sup>31,32</sup> | tag: 9.0 × 2.1 mm, 0.087 g, 134.2 kHz                                                | Biomark                                                    | <a href="http://www.biomark.com/">http://www.biomark.com/</a>                                                                                                                 | 2011-2014 | 0.08                    | 19                   | 200            | 157                          |
|                                                  | RFID: custom made                                                                    | Calima Engineering, & Max Planck Institute for Ornithology | <a href="http://www.calima.de">http://www.calima.de</a><br><a href="http://www.orn.mpg.de/en">http://www.orn.mpg.de/en</a>                                                    |           |                         |                      |                |                              |
|                                                  | temperature probe: TinyTag Talk PB-5005-0M6 (ø 2.5 mm) with Talk 2 logger TK-4023 or | Gemini Data Loggers Ltd                                    | <a href="http://www.tinytag.info">www.tinytag.info</a>                                                                                                                        |           |                         |                      |                |                              |
|                                                  | MSR® (12 × 6 mm) with MSR® 145 logger                                                | MSR® Electronics GmbH                                      | <a href="http://www.msr.ch/">http://www.msr.ch/</a>                                                                                                                           |           |                         |                      |                |                              |
|                                                  | tag: 11.5 × 2.12 mm, 0.1 g, 125 kHz                                                  | Trovan®                                                    | <a href="http://www.trovan.com">http://www.trovan.com</a>                                                                                                                     | 2007      | 5                       | 1                    | 3              | 3                            |
|                                                  | RFID: custom made                                                                    | EID Aalten BV                                              | <a href="http://www.dorset.nu/en/">http://www.dorset.nu/en/</a>                                                                                                               |           |                         |                      |                |                              |
| RFID + tag glued to the tail <sup>33</sup>       | temperature probe: TinyTag Talk PB-5005-0M6 (ø 2.5 mm) with Talk 2 logger TK-4023    | Gemini Data Loggers Ltd                                    | <a href="http://www.tinytag.info">www.tinytag.info</a>                                                                                                                        |           |                         |                      |                |                              |
|                                                  | tag: 11.5 × 2.12 mm, 0.09g, 128 kHz                                                  | Trovan®                                                    | <a href="http://www.trovan.com">http://www.trovan.com</a>                                                                                                                     | 2005-2008 | 1.7-5.5                 | 1                    | 34             | 34                           |
|                                                  | RFID: LID650 with extended memory, driver TM613, Antenna ANT614                      |                                                            |                                                                                                                                                                               |           |                         |                      |                |                              |
|                                                  | tag: TIRIS 12 × 6 × 3 mm, 0.4 g, 134.2 kHz                                           | Texas Instruments                                          | <a href="http://www.ti.com">http://www.ti.com</a>                                                                                                                             | 1997      | 1/3                     | 1                    | 6              | 6                            |
|                                                  | RFID: TIRIS Micro-reader                                                             |                                                            |                                                                                                                                                                               |           |                         |                      |                |                              |
|                                                  | TIRIS tag: 12 × 6 × 3 mm, 0.4 g, 134.2 kHz                                           | Texas Instruments                                          | <a href="http://www.ti.com">http://www.ti.com</a>                                                                                                                             | 2006      | 1/3                     | 1                    | 18             | 18                           |
| Light logger <sup>34,35,68</sup>                 | RFID: custom made                                                                    | Francis Scientific Instruments Limited                     | <a href="https://www.duedil.com/comp-any/01964877/francis-scientific-instruments-limited">https://www.duedil.com/comp-any/01964877/francis-scientific-instruments-limited</a> |           |                         |                      |                |                              |
|                                                  | MK10, 12, 14 18, 20: 0.7-1.4g, light scale 0-64 (64 ≥ 100 lux)                       | British Antarctic Survey, currently Biotrack               | <a href="http://www.biomark.com/">http://www.biomark.com/</a>                                                                                                                 | 2008-2013 | 2-10                    | 48                   | 261*           | 55                           |
|                                                  | Intigeo W65A9RK: 0.7g, absolute light levels (lux)                                   | Migrate Technology Ltd                                     | <a href="http://www.migratetech.co.uk">http://www.migratetech.co.uk</a>                                                                                                       | 2012-2014 | 5-10                    | 23                   | 136*           | 11                           |
| GPS-tracker <sup>36</sup>                        | UvA-BITS 4C: 62 × 30 × 12, 14 g                                                      | University of Amsterdam                                    | <a href="http://www.uva-bits.nl/">http://www.uva-bits.nl/</a>                                                                                                                 | 2010      | 10-30                   | 1                    | 8              | 8                            |
|                                                  | UvA-BITS 2CDse: 52 × 22 × 9, 7.5 g                                                   |                                                            |                                                                                                                                                                               | 2014      | 20                      | 1                    | 1**            | 0                            |
| Radio-transmitter <sup>24</sup>                  | iTag: 26 × 15 × 9 mm, 4 g                                                            | e-obs GmbH                                                 | <a href="http://www.e-obs.de/">http://www.e-obs.de/</a>                                                                                                                       | 2009      | 0.07                    | 2                    | 3              | 3                            |
| Video <sup>69-72</sup>                           |                                                                                      |                                                            |                                                                                                                                                                               | 2005-2006 | 1/3                     | 1                    | 28             | -                            |
|                                                  |                                                                                      |                                                            |                                                                                                                                                                               | 2005-2011 | constant                | 3                    | 25             | -                            |
| Observations                                     |                                                                                      |                                                            |                                                                                                                                                                               | 1994      | 30                      | 1                    | 5              | -                            |
|                                                  |                                                                                      |                                                            |                                                                                                                                                                               | 2011      | constant                | 1                    | 3              | -                            |

For details about methods used in each populations, see supplementary data of ref. 53.

\*At one nest a bird with a MK logger was recaptured and the logger exchanged for an Intigeo logger. This nest appears in *n* for both logger types.

\*\*Simultaneously equipped with light-logger (Intigeo). This nest appears in *n* for both GPS-tracker and Intigeo.

**Extended Data Table 2 | Effects of phylogeny and sampling on bout length and period length**

| Response        | Effect type       | Effect        | Posterior mode | 95% CI |       | N (range)       |
|-----------------|-------------------|---------------|----------------|--------|-------|-----------------|
|                 |                   |               |                | Lower  | Upper |                 |
| Median bout [h] | Fixed             | Intercept     | 7.2            | 1.04   | 12    | 1100 (924-2079) |
|                 |                   | Sampling      | 0.16           | -0.2   | 0.61  | 1100 (809-1644) |
|                 | Random (variance) | Phylogeny     | 25.33          | 4.6    | 59.6  | 1100 (753-1383) |
|                 |                   | Species       | 0.01           | 0      | 12.1  | 1100 (779-1636) |
|                 |                   | Breeding site | 2.13           | 0.96   | 4.28  | 1100 (808-2242) |
|                 |                   | Residual      | 5.04           | 4.51   | 5.61  | 1100 (838-1444) |
|                 | Pagel's $\lambda$ |               | 1              | 0.5    | 1     | 1100 (814-1316) |
|                 |                   |               |                |        |       |                 |
| Period [h]      | Fixed             | Intercept     | 21.94          | 12.8   | 30.67 | 1100 (765-1392) |
|                 |                   | Sampling      | 0.13           | -0.41  | 0.65  | 1100 (741-1468) |
|                 | Random (variance) | Phylogeny     | 66.22          | 14.3   | 153   | 1100 (729-1638) |
|                 |                   | Species       | 0.06           | 0      | 29.36 | 1100 (729-1435) |
|                 |                   | Breeding site | 0.01           | 0      | 0.88  | 1100 (814-1378) |
|                 |                   | Residual      | 14.87          | 13.3   | 16.84 | 1100 (884-1460) |
|                 | Pagel's $\lambda$ |               | 1              | 0.54   | 1     | 1100 (740-1523) |
|                 |                   |               |                |        |       |                 |

The posterior estimates (modes) of the effect sizes with the highest posterior density intervals (95% CI) and the median and range of the effective sample sizes (N (range)) come from the joint posterior distribution of 100 separate runs each with 1 of 100 separate phylogenetic trees from <http://birdtree.org>.  $n_{\text{bout}} = 729$  nests from 91 populations belonging to 32 species.  $n_{\text{period}} = 584$  nests from 88 populations belonging to 30 species. Sampling (how often the incubation behaviour was sampled) was ln-transformed and then mean-centred and scaled (divided by s.d.). For procedures and specifications related to phylogenetic Bayesian mixed models see Methods. Estimating Pagel's  $\lambda$  on the species level ( $n_{\text{bout}} = 32$  species,  $n_{\text{period}} = 30$  species) with phylogenetic generalized least-squares using the function 'pgls' from the R package caper<sup>73</sup> gave similar results (median (range)  $\lambda_{\text{bout}} = 0.73$  (0.63–1) and  $\lambda_{\text{period}} = 0.95$  (0.64–1), based on 100 estimates each for 1 of the 100 trees).



**Extended Data Table 4 | Effect of latitude, body size, escape distance and life history on biparental incubation rhythms in shorebirds**

| Response                                         | Effect type       | Fixed effects         | Posterior mode | 95% CI |       | N (range)       |
|--------------------------------------------------|-------------------|-----------------------|----------------|--------|-------|-----------------|
|                                                  |                   |                       |                | Lower  | Upper |                 |
| Bout [h]                                         | Fixed             | Intercept             | 7.45           | 2.65   | 12    | 1100 (804-1496) |
|                                                  |                   | Wing length           | -0.78          | -2.5   | 1.05  | 1100 (839-1638) |
|                                                  |                   | Latitude              | 1.72           | 0.63   | 2.65  | 1100 (850-1642) |
|                                                  |                   | Escape distance       | -1.68          | -3.3   | -0.25 | 1100 (634-2046) |
|                                                  | Random (variance) | Phylogeny             | 0.19           | 0      | 45    | 1100 (803-1875) |
|                                                  |                   | Species               | 0.07           | 0      | 14.4  | 1100 (695-1580) |
|                                                  |                   | Breeding site         | 1.4            | 0.59   | 3.02  | 1100 (833-1480) |
|                                                  |                   | Residual              | 5.02           | 4.53   | 5.64  | 1100 (516-1916) |
|                                                  | Page's $\lambda$  |                       | 0.72           | 0.13   | 1     | 1100 (731-1407) |
| Light entrainable rhythm [1,0] on binomial scale | Fixed             | Intercept             | -1.62          | -3.19  | -0.13 | 1100 (731-1633) |
|                                                  |                   | Latitude              | -0.56          | -1.15  | -0.07 | 1100 (765-1575) |
|                                                  | Random (variance) | Phylogeny             | 0.05           | 0      | 5.54  | 1100 (883-1371) |
|                                                  |                   | Species               | 0.02           | 0      | 2.68  | 1100 (965-2246) |
|                                                  |                   | Breeding site         | 0              | 0      | 0.63  | 1100 (605-1304) |
|                                                  | Page's $\lambda$  |                       | 0.74           | 0.02   | 1     | 1100 (932-1498) |
| Absolute deviations from 24-h                    | Fixed             | Intercept             | 0.17           | -0     | 0.35  | 1100 (459-1501) |
|                                                  |                   | Latitude              | 0.03           | -0     | 0.07  | 1100 (777-1488) |
|                                                  | Random (variance) | Phylogeny             | 0              | 0      | 0.07  | 1100 (786-1393) |
|                                                  |                   | Species               | 0              | 0      | 0.03  | 1100 (861-1412) |
|                                                  |                   | Breeding site         | 0              | 0      | 0     | 1100 (826-1860) |
|                                                  |                   | Residual              | 0.03           | 0.03   | 0.04  | 1100 (948-2039) |
|                                                  | Page's $\lambda$  |                       | 0.74           | 0.02   | 1     | 1100 (843-1471) |
| Deviations from 24-h                             | Fixed             | Intercept (non-tidal) | 0.02           | -0.04  | 0.09  | 1100 (851-1742) |
|                                                  |                   | Life history (tidal)  | -0.02          | -0.1   | 0.04  | 1100 (702-2257) |
|                                                  | Random (variance) | Phylogeny             | 0              | 0      | 0.01  | 1100 (806-1692) |
|                                                  |                   | Species               | 0              | 0      | 0     | 1100 (692-1601) |
|                                                  |                   | Breeding site         | 0              | 0      | 0.01  | 1100 (656-1490) |
|                                                  |                   | Residual              | 0.07           | 0.06   | 0.08  | 1100 (760-1563) |
|                                                  | Page's $\lambda$  |                       | 0.77           | 0.01   | 1     | 1100 (864-1451) |

The posterior estimates (modes) of the effect sizes with the highest posterior density intervals (95% CI) and the median and range of the effective sample sizes (N (range)) come from the joint posterior distribution of 100 separate runs each with 1 of the 100 separate phylogenetic trees from <http://birdtree.org>.  $n_{\text{bout}} = 729$  nests from 91 populations belonging to 32 species. For models on light-entrainable rhythm, absolute deviations and deviations from 24 h:  $n = 584$  nests from 88 populations belonging to 30 species. Latitude (in bout model: absolute value), wing length (ln-transformed), and escape distance (ln-transformed) were mean-centred and scaled (divided by s.d.). The estimates for the light-entrainable rhythm are on a binomial scale. For procedures and specifications related to phylogenetic Bayesian mixed models see Methods.