A tropical bird can use the equatorial change in sunrise and sunset times to synchronize its circannual clock

Wolfgang Goymann1,*, Barbara Helm2,3, Willi Jensen1, Ingrid Schwabl1 and Ignacio T. Moore4

1Max-Planck-Institut für Ornithologie, Abteilung für Verhaltensneurobiologie, Eberhard-Gruenewald-Straße 6A, 82319 Seewiesen, Germany
2Fachbereich Biologie, Universität Konstanz, Postfach 616, 78457 Konstanz, Germany
3Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Graham Kerr Building, Glasgow G12 8QQ, UK
4Department of Biological Sciences, Virginia Tech, 2119 Derring Hall, Blacksburg, VA 24060, USA

At higher latitudes, most organisms use the periodic changes in day length to time their annual life cycle. At the equator, changes in day length are minimal, and it is unknown which cues organisms use to synchronize their underlying circannual rhythms to environmental conditions. Here, we demonstrate that the African stonechat (Saxicola torquatus axillaris) — an equatorial songbird — can use subtle solar cues for the annual timing of postnuptial molt, a reliable marker of the circannual cycle. We compared four groups that were kept over more than 3 years: (i) a control group maintained under constant equatorial day length, (ii) a 12-month solar time group maintained under equatorial day length, but including a simulation of the annual periodic change in sunrise and sunset times (solar time), (iii) a 14-month solar time group similar to the previous group but with an extended solar time cycle and (iv) a group maintained under a European temperate photoperiod. Within all 3 years, 12-month solar time birds were significantly more synchronized than controls and 14-month solar time birds. Furthermore, the molt of 12-month solar time birds occurred during the same time of the year as that of free-living Kenyan conspecifics. Thus, our data indicate that stonechats may use the subtle periodic pattern of sunrise and sunset at the equator to synchronize their circannual clock.

Keywords: circannual rhythm; equation of time; photoperiod; molt Zeitgeber; life cycle

1. INTRODUCTION

For seasonal organisms, the annual change in day length (photoperiod) represents the most reliable predictive cue for the timing of life-cycle stages. For example, many birds at temperate and high latitudes show circannual rhythms that are synchronized by photoperiodic information as the main Zeitgeber (a synchronizing external cue; [1]). This synchronization is crucial for the proper timing of life-history stages and activities such as migration, breeding and molt (the annual loss and replacement of feathers that is an essential part of the life cycle of birds) [2–5]. The strength of photoperiod as a Zeitgeber is demonstrated by the fact that some species can entrain to photoperiodic cycles that differ greatly from the circannual rhythms [15], but in nature, their life-cycle stages occur annually. In Kenya, breeding is limited to the rains around March to June and is followed by postnuptial molt that starts at the end of June and continues until mid-November [16] (see also phenology data in figure 1). Gwinner & Scheuerlein [14] addressed this topic in a tropical songbird, the African stonechat (Saxicola torquatus axillaris). Stonechats show robust endogenous circannual rhythms [15], but in nature, their life-cycle stages occur annually. In Kenya, breeding is limited to the rains around March to June and is followed by postnuptial molt that starts at the end of June and continues until mid-November [16] (see also phenology data in figure 1). Gwinner & Scheuerlein [14] demonstrated experimentally that changes in day light intensity (i.e. mimicking the annual pattern in cloud cover during the rainy and dry seasons) may provide synchronizing cues. However, cloud cover is very variable within and between years and hence may not be precise. There is, however, an alternative photic cue that is more predictive and could be used as Zeitgeber: while day length is constant at the equator, the times of sunrise and sunset fluctuate in parallel by about 30 min over the year with two recurring annual maxima and minima (referred to in astronomy as the ‘equation of time’; figure 1 and supplementary discussion 1 in Borchert et al. [12]). This annual fluctuation is caused by the elliptic shape of the...
Earth’s orbit around the sun and the tilt of the Earth’s axis relative to its orbit and corresponds to the difference between apparent solar time and the mean time. As a slight but reliable environmental cue, it is consistent from year to year and independent of climate, but so far it is unknown whether animals can use this cue to time their life cycle. It has been suggested that—close to the equator—tropical trees synchronize flowering according to the annual change in the time of sunrise and sunset or associated changes in insolation [12,17]. In view of the sensitivity of birds to subtle photic cues [9,18], we hypothesized that they may be able to entrain to the annual pattern of sunrise and sunset times at the equator (hereafter called ‘solar time’).

To test this hypothesis, we examined synchronicity in four experimental groups of African stonechats of equatorial origin that were kept under different photic conditions. We exposed one group to a constant equatorial photoperiod (constant day length) and simulated the annual variation in sunrise and sunset time at the equator (12-month solar time group; upper graph in figure 2b). As a control to assess the birds’ behaviour in the absence of any *Zeitgeber*, a second group was kept under the same constant equatorial photoperiod but without simulating the annual change in sunrise and sunset times (constant time group; upper graph in figure 2a). To further investigate the ability of stonechats to synchronize to solar time, we exposed a third group to this potential *Zeitgeber* but weakened its strength by extending the *Zeitgeber* period to 14 months (14-month solar time group; upper graph in figure 2c). Because postnuptial moult was previously found to be a reliable marker for the annual cycle of stonechats [19–21], we used individual timing patterns of moult as a measure of synchronization. We further compared the synchronicity of postnuptial moult of these three groups with that of a fourth group, consisting of African stonechats studied earlier by our team under a naturally changing European photoperiod (upper graph in figure 3). The published studies had shown that this photoperiodic condition acts as strong *Zeitgeber* [20,22,23] and are therefore used here as a positive reference for tight synchronization (via extraction of information on synchronicity from the original data).

We predicted that whether variation in sunrise and sunset functioned as a *Zeitgeber*, moult of birds in the 12-month solar time group should cycle with the *Zeitgeber* period length of 12 months and should be synchronous between individuals as measured by a synchronicity index (defined as the per cent overlap in the timing of moult between individuals). Moult in this group should occur at a similar time relative to the *Zeitgeber* as it does in free-living Kenyan conspecifics (i.e. show a similar phase-angle difference (Δφ) relative to the periodic change in sunrise and sunset times as in free-living conspecifics [16] (see also figure 1). In contrast, birds in the constant time group should free run with respect to each other and to external time, i.e. there should be little synchronicity among birds and no synchronicity to external time. The 14-month solar time group was used to further examine possible *Zeitgeber* characteristics of solar time. If birds are able to entrain to this extended and weaker cycle (with smaller changes in solar time per unit of time when compared with the 12-month solar time group), then they should synchronize to each other and to a 14-month cycle, or else, show individual free-running rhythms.

Differences between the three solar time groups should develop over time, as free-running birds would follow their individual schedules, so that the last recorded cycles should yield the clearest contrasts. Furthermore, moult in birds can proceed independently for body plumage and flight feathers [24]. In the absence of a *Zeitgeber*, the two processes may dissociate, and flight feather moult in particular can be omitted [14,25,26]. We therefore use dissociation of the two moult processes as further evidence of weak or absent entrainment.

2. METHODS
(a) Study animals
Originally, we used 24 African stonechats, all of which were descendants of a resident population imported from Nakuru, Kenya (0°14′S, 36°0′E; 2500 m a.s.l.) in 1999. Six birds hatched in 1999 were collected as nestlings in Kenya, the other birds were bred and raised in captivity in 2001 (n = 1), 2002 (n = 3), 2003 (n = 7), 2004 (n = 1) and 2005 (n = 6). Before the experiment, all birds were maintained and synchronized under the local photoperiod of Erling-Andechs, Germany (47.5°N). On 5 August 2005, during postnuptial moult, the birds were moved to three identical indoor rooms. Birds of different sex and age classes and siblings were equally distributed among rooms so that these factors would not bias results. Three additional stonechats entered the experiment in October and December 2005 and in March 2006 (hatched in 1999 and 2004) to replace birds that had died. The birds received our standard diet [27] and were kept in individual cages (60 × 35 × 45 cm) where they could hear but not see each other until January 2009. In addition, we used data from 13 African stonechats collected in Kenya that were maintained under a European photoperiod in the same temperature-controlled indoor rooms from 1982 to 1984. These African stonechats were studied from fledging until the completion of their second adult moult. We include data from five females and eight males (for details on these birds see earlier studies [20,22]).

(b) Experimental rooms and treatment
Birds were kept in three adjacent sound-proof and temperature-controlled rooms connected to the same ventilation system [18]. Each room was equipped with two halogen lamps with dimmable 150 W Osram Haloline 646 959 bulbs (colour rendering index 100, colour temperature 3000 K). The lamps were mounted in line with the cages, so that the birds received light only indirectly from a white reflecting wall opposite the light source, i.e. birds could not get any ‘celestial cues’ from the two light sources. Light intensity was approximately 400 lux at the front of each cage. During the night, several small light bulbs ensured indirect ‘moonlight’ illumination of 0.01 lux. Room temperature in all rooms ranged between 18 °C and 20 °C during the night and from 22 to 25 °C during the day. The photoperiod in all three rooms was 12.07 h of light plus two 25 min periods of dawn and dusk during which light intensity gradually increased or decreased from 0.01 (night level) to 400 lux (day level). These conditions simulated the natural day length including dusk and dawn (based on civil twilight) at an elevation of 2500 m a.s.l. at the equator, corresponding
to the altitude at Nakuru, Kenya. The first room housed the constant time group. Here, the timing of sunrise and sunset was kept constant throughout the year with dawn starting at 06.05 (full daylight at 06.30) and dusk starting at 18.37 (full night at 18.02; figure 2a). Day length and sunrise times were calculated with Astronomy Lab 2 (Personal MicroCosms, Greenwood Village, CO 80112, USA). The second room housed the 12-month solar time group. This group received a simulation of the annual variation in sunrise and sunset time at the equator: the onset of dawn started between 05.51 and 06.22 (full day light between 06.16 and 06.47) and onset of dusk between 18.23 and 18.54 (night between 18.48–19.19; figure 2b). In the third room, birds received a simulation of the annual variation in sunrise/sunset time, but the natural cycle of 12 months was lengthened to 14 months (14-month solar time group; figure 2c). The changes in sunrise and sunset times were implemented in weekly intervals in steps ranging from 0 to 3 min depending on the steepness of the cycle (figures 1 and 2). In addition, we compared the data from these three groups with a fourth group of 13 African stonechats that had been maintained under the photoperiodic conditions of migratory European stonechats at 47.5° N during summer and 40° N during winter in a previous study (see earlier studies [20,22,23]). In these birds, day length was adjusted weekly assuming that they reach 45° on 4 October, 42.5° on 11 October and 40° on 18 October (figure 3). In spring, birds were assumed to reach 42.5° on 28 February, 45° on 7 March and 47.5° on 14 March. In these birds, there was no simulation of dawn and dusk, but light intensity was similar to the other three groups with 0.01 lux at night and 400 lux during the day.

To examine entrainment to the change in sunrise and sunset time, we quantified the phase-angle difference (ϕ) of moult onset to the putative Zeitgeber cycle as follows. As reference phase, we chose the date on which sunrise and sunset were timed the latest (Julian date 41, i.e. 10 February; figure 1). Based on published field data from free-living Kenyan stonechats, moult started on 30 June (calculated as the mean date between captures of free-living stonechats that did not yet moult and the first captures that showed substantial moult (see our fig. 1 and fig. 4d,e in Dittami & Gwinner [16])). This yielded a phase-delayed and, hence negative, phase-angle difference ϕ of −141 days.

(c) Moult parameters and statistical analysis

For the duration of the study, every two to three weeks we recorded—for each bird—the state of moult for body and flight feathers separately. We assessed the state of body moult by noting feather growth in any of the 19 different feather tracts on the bird’s body [28]. We defined the onset of body moult as the mean date between the last recording without moult and the first day on which moult was detected in at least four of the 19 feather tracts. End of moult was defined as the mean date between the last recording with moult finished in at least 15 of the 19 feather tracts and the first day without moult. Flight feather moult was scored following [29]. All 10 primaries and all nine secondary wing feathers were scored on a scale from 0 (old feathers) to 5 (fully grown new). Scores were averaged over the two wings resulting in values ranging from 0 to 10 (all feathers old) to 95 (all feathers new). Onset of flight feather moult was defined as the mean date between the last recording without flight feather moult and the first day on which at least one primary or secondary moulted, and completion was defined as the mean date between the last recording with moult and the first recording without moult. For each year and within each group, we then measured the proportion of overlap in moult of each individual with each other individual. An example illustrates how the proportion of overlap in moult was calculated: let us assume we have two individuals A and B. A moult from day 50 to 100, and B moult from day 75 to 150. This means that the moult of individual A overlaps during 50 per cent of its total duration. During 50 per cent of its total duration with the moult of individual B. However, the moult of individual B overlaps only 33.3 per cent of its total duration with that of individual A. From these individual values, we then calculated the mean for each individual, which gives the moult synchronicity index of each individual within its group (figure 4). This moult synchronicity index was then compared between groups using a non-parametric Kruskal–Wallis test and Conover post hoc tests [30]. Non-parametric tests were used because they are more conservative and with small sample sizes normality tests are not very reliable. However, parametric tests (generalized-linear mixed model) rendered similar results. For the calculation, we used data only for individuals that had entered the experiment at the latest in April 2006 and that had completed all cycles from the beginning of the experiment until the period of analysis (first, second and third year). The sample sizes for the first, second and third year were 7, 7 and 6 for the constant time group, 7, 7 and 5 for the 12-month solar time group, and 5, 4 and 4 for the 14-month solar time group (see also table 1). We also created mean body and flight feather moult curves of individuals within each treatment group by taking the mean score of a 20-day period. Smoothing was performed by calculating a moving average over five adjacent 20-day periods. A regular sinusoidal curve with
one peak per year indicates synchronization to an external cue with the magnitude of the amplitude reflecting the degree of synchronization among birds within a group: a high amplitude indicates that the birds of one group are synchronous to each other whereas a low amplitude indicates low synchronicity among birds. In contrast, an irregular curve with various peaks per year indicates free-running rhythms, i.e. each bird follows its own endogenous schedule without synchronization to an external Zeitgeber cue.

To calculate the period length $\tau$ of moult cycles between the second and third year, we used body moult only, because several birds of the constant time and 14-month solar time group showed irregular patterns or skipped flight feather moult. Period length $\tau$ for each bird was measured by calculating the difference between moult completion date in the third year and moult completion date in the second year. Statistical comparisons were conducted with SYSTAT 13 at an $\alpha$-level of 0.05 (two-tailed). To minimize the loss of birds along the experiment, we did not measure gonad size that requires invasive surgery, nor puncture the birds’ veins for repeated blood sampling.

3. RESULTS

We found that during the first cycle, for which we had predicted weak differences between treatments, the groups differed significantly in synchronicity of body moult (Kruskal–Wallis test $H_{body moult} = 25.80, p < 0.0001$). The body moult was significantly more synchronous between birds exposed to a European photoperiod than between birds of all other groups (post hoc Conover tests: all $ps < 0.0001$). Birds of the 12-month solar time group were significantly more synchronous to each other than birds of the 14-month solar time group ($p = 0.01$ and tended to be more synchronous than birds in the constant control group ($p = 0.08$; table 1, figures 2 and 3). Flight feather moult also differed significantly in synchronicity between groups ($H = 13.03, p < 0.002$), being significantly higher in the 12-month solar time group than in the control ($p < 0.001$) and the 14-month solar time group ($p < 0.001$; table 1, figures 2 and 3). Birds maintained under a European photoperiod were not included in this comparison because their first cycle, post-juvenile moult, did not involve replacement of flight feathers (figure 3).

During the second cycle, synchronicity of body and flight feather moult also differed significantly between the groups ($H_{body moult} = 10.55, p = 0.0001$; $H_{flight feather moult} = 22.20, p < 0.0001$; figures 2 and 3). Body and flight feather moult of birds under a European photoperiod was more synchronous than those of birds in all other groups (all $ps < 0.0001$). Furthermore, synchronicity of flight feather moult was significantly higher in birds of the 12-month solar treatment than in birds of the constant control group ($p = 0.02$) and the 14-month solar time group ($p = 0.007$; table 1, figures 2 and 3).

In the third and last year, the synchronicity of both body and flight feather moult differed significantly between treatments ($H_{body moult} = 20.45, p < 0.0002$, $H_{flight feather moult} = 19.59, p = 0.0002$): body and flight feather moults of birds in the 12-month solar time group were significantly more synchronous than those of the constant time and the 14-month solar time group (figures 2–4, table 1), but less so than in the group of African stonechats entrained to the European photoperiod (figures 3 and 4, table 1).

Furthermore, in contrast to birds of the constant time and the 14-month solar time group, birds of the 12-month solar time group showed coupled patterns of body and flight feather moult in all years (figure 2), indicating a common Zeitgeber for the different kinds of moult. Another indicator of a common Zeitgeber were the smoothed averages of body and flight feather moult in the 12-month solar time group (blue and orange curves in figure 2b): similar to the European photoperiod group (figure 3), the 12-month solar time group showed a regular pattern with one clear sinusoidal moulting peak per year (figure 2b), indicating synchronization among birds and within each year. The sinus amplitude of the European photoperiod group was higher than the amplitude of the 12-month solar time group, demonstrating that photoperiod is a stronger Zeitgeber than solar time. In contrast to these two groups, the constant control group and the 14-month solar time group showed irregular smoothed average curves without a clear annual peak in combination with low amplitudes (figure 2a,c), thus indicating low synchronicity among birds, suggesting that each bird followed its own free-running rhythm.

Period length of the body moult cycle between the second and third year was closest to the expected 365 days in birds maintained under a European photoperiod and in the 12-month solar time group (figure 5). The coefficient of variation (CV) in period length was lowest in the group maintained under a European photoperiod (CV = 0.05), intermediate for the 12-month solar time group (CV = 0.16) and highest for the groups maintained under 14-month solar time (CV = 0.34) and constant time conditions (CV = 0.33). For flight feather moult, we could not calculate the period length between...
Figure 2. Body moult (blue bars) and flight feather moult (orange bars) of African stonechats maintained under an equatorial photoperiod for almost 3½ years. The thin (brown) lines indicate the total time each individual bird stayed in the experiment. The time axis represents consecutive days (1 denotes 1 January 2005). The experiment started in August 2005 (day 215) and ended in January 2009 (day 1500). Depicted are three groups of birds which either received (a) no change in the timing of sunrise and sunset (constant time conditions; upper graph in (a), (b) a simulation of the natural, 12-month cycle in the change of sunrise and sunset times at the equator (12-month solar time conditions, upper graph in (b); only change in sunrise shown, but sunset changes accordingly) and (c) a simulation of the annual pattern in sunrise and sunset times at the equator stretched to 14 months (14-month solar time conditions; upper graph in (c); only sunrise shown). The blue and orange curves represent smoothed averages of body moult and flight feather moult scores of all individuals within one group (represented on the right y-axis scale; see methods for the details of how the smoothed averages were calculated), respectively. A sinusoidal curve with one peak per year indicates synchronization to an external annual Zeitgeber with the magnitude of the amplitude reflecting synchronicity among birds within one group. A curve with several peaks per year indicates the absence of synchronization to an external Zeitgeber. Please note that owing to differences in scoring method the amplitude of body moult (blue) is naturally smaller than the amplitude of flight feather moult (orange). The dashed vertical lines indicate the external years in (a,b) and the prolonged 14 month ‘year’ in (c). (b) Black vertical arrows in the upper graphs indicate the onset of moult in free-living stonechats at Nakuru, Kenya. (c) Vertical arrows indicate the expected onset of moult if the birds would have synchronized to a 14-month solar time period. Both the vertical dashed lines and the arrows serve as orientation how rhythms should be arranged if they were entrained. Note that all birds were initially synchronized to a European photoperiod before they entered the experiment (with most birds still molting when entering the experiment around day 215). Bird IDs starting with ‘f’ represent females, those starting with ‘m’ represent males.

the second and third year for the constant time and the 12-month solar time group, because some birds showed irregular moult patterns. By contrast, all birds of the 14-month solar time group showed a consistent pattern of flight feather moult with a period close to one year (mean period $\pm$ 95% CI: 360.8 $\pm$ 60.3 days, CV = 0.13).
Figure 3. Body moult (blue bar) and flight feather moult (orange bar) of African stonechats maintained under a European photoperiod (upper graph with the red line indicating the length of the daily period with lights-on) from hatching (approx. day 115) until the end of their third year of life. The time axis represents consecutive days (1 denotes 1 January 1982). The thin brown line indicates the total time each individual bird stayed in the experiment. The blue and orange curves represent smoothed averages of body moult and flight feather moult scores (represented on the right y-axis scale; see methods for the details of how the smoothed averages were calculated), respectively. A sinusoidal curve with one peak per year indicates synchronization to an external annual Zeitgeber with the magnitude of the amplitude reflecting synchronicity among birds. A curve with several peaks per year indicates the absence of synchronicity among birds. Together, these results indicate that birds maintained under the 12-month solar time condition were more closely synchronized to the 365 day cycle than the birds of the constant and 14-month solar time period, but less so than birds maintained under a European photoperiod.

Onset of moult in birds of the 12-month solar time group was timed similarly as in free-living conspecifics. For free-living Kenyan stonechats, flight feather and body moult was observed to start 141 days after the body moult of equatorial stonechats during the third year of the experiment (median and interquartile range). Birds maintained under a simulation of the natural 12-month change in sunrise and sunset times at the equator (12-month solar time group) showed an intermediate pattern of moult synchrony. They were significantly more synchronous than birds kept under equatorial conditions with a constant time in sunrise and sunset (constant time group), and birds maintained under a simulation of the change in sunrise and sunset times extended to a 14-month period (14-month solar time group). At the same time, they were less synchronous than equatorial stonechats maintained under a northern temperate European photoperiod (Kruskal–Wallis test with post hoc comparisons following Conover [30]).

Figure 4. (a) Synchronicity of flight feather and (b) body moult of equatorial stonechats during the third year of the experiment (median and interquartile range). Birds maintained under a simulation of the natural 12-month change in sunrise and sunset times at the equator (12-month solar time group) showed a pattern of moult synchrony. They were significantly more synchronous than birds kept under equatorial conditions with a constant time in sunrise and sunset (constant time group), and were less synchronous than birds maintained under a northern temperate European photoperiod (Kruskal–Wallis test with post hoc comparisons following Conover [30]).

4. DISCUSSION

Our findings support the hypothesis that the annual change in the timing of sunrise and sunset is a potential Zeitgeber for circannual rhythms of equatorial birds. In the absence of any change in day length, stonechats in the 12-month solar time group entrained to the subtle shift of the solar day and assumed a phase relationship to the Zeitgeber that was similar to the situation observed in free-living birds [16]. Compared with the photoperiodic cues of a northern temperate photoperiod this Zeitgeber was relatively weak, potentially allowing other environmental cues (e.g. cloud cover [14] or slight changes in the duration of dawn and dusk [18,31]) to further modify the circannual rhythm. When this subtle Zeitgeber was further reduced in strength by changing its period length from a natural 12-month solar time cycle to a 14-month solar time cycle (and consequently attenuated changes in sunrise and sunset times), entrainment was absent. Because the stonechats’ endogenous circannual rhythm is usually 9–10 months [15] and entrainment gets weaker the further the Zeitgeber period differs from the endogenous period [7] birds in the 14-month solar...
synchronized in nature had remained unclear although previously been suggested to time the synchronicity in circannual cycles under permissive conditions [19,21,25], but how these cycles develop only under permissive conditions, i.e. African stonechats showed circannual cycles under a constant photoperiod with 12.25 hrs of light, but 70 per cent of them ceased to cycle with a constant photoperiod of 12.8 hrs of light without simulated dawn and dusk [25].

Similar to many other longer-lived tropical organisms, African stonechats at the equator express a highly seasonal annual life cycle with reproduction during the rainy season and subsequent moult when the young become independent [16,32]. In captivity, African stonechats show strong and robust endogenous circannual cycles under permissive conditions [19,21,25], but how these cycles are synchronized in nature had remained unclear although changes in day light intensity owing to annual cycles of cloud cover may play a role [14]. Our data suggest that the annual pattern of sunrise and sunset time at the equator may be a sufficient environmental cue to function as a Zeitgeber. We are aware of only one other experimental study that examined entrainment to an annual cycle of sunrise and sunset times. The study species, Anousa geoffroyi, a tropical bat, failed to synchronize its circannual rhythm to a nine-month cycle, or in fact to any kind of photoperiodic simulation [33].

It is highly unlikely that the higher synchronicity of the 12-month solar time group was caused by an external stimulus other than the change in the timing of sunrise and sunset. All three experimental rooms were adjacent to each other, were connected to the same ventilation, electrical and light-control systems, sex and age classes were similar between the rooms, and all birds were fed and cages cleaned at the same time of the day. Thus, any disturbance would have affected all three rooms equally. Furthermore, any synchronization owing to vocal interactions (the birds could not see each other!) should have been similar in all experimental rooms. Before the experiment, all birds were maintained under a European photoperiod, which represents a very strong Zeitgeber cue, potentially explaining why it took the 12-month solar time birds three cycles to fully synchronize to the weaker Zeitgeber.

The mechanistic details of circannual rhythms and their entrainment to Zeitgeber are still poorly understood. However, in a number of organisms from beetles to mammals [34–36], it has become clear that circannual clocks respond to photic cues in a phase-dependent way. This may explain how African stonechats could breed annually despite the biannual changes in sunrise and sunset times. Stonechats are highly responsive to slight differences in photic cues during specific times of year [37], while during other periods of the year their reproductive system shows little or no response to stimulatory light conditions [14]. If accommodated to equatorial light conditions, then circannual phase responses could function as a filter that enables the birds to respond to only one annual recurrence of inductive light conditions. Such putative filter effects of circannual rhythms would fit well with current thinking of their adaptive significance [38,39]. Recent research, most visibly in the context of rapid global change, has documented the fitness costs of mismatches between seasonal behaviours and environmental cycles. The ability of organisms to avoid such mismatches hinges on their ability to correctly predict and anticipate environmental seasonality, not only at high latitudes but also in seasonal tropical habitats such as those used by African stonechats [15,16]. On their Kenyan breeding grounds, the occurrence of rainy and dry seasons is predictable over a range of several years, and timely preparation for breeding may give birds a valuable head start for maximizing reproductive output during the short time of high insect availability. Compared with photoperiodically predictable high-latitude habitats, it is more difficult at the equator to anticipate the time of highest likelihood of rains and to buffer against breeding after spurious, short rains. Being able to use subtle solar cues to predict correctly upcoming seasons could therefore provide survival and reproductive value, and thus enhance fitness [39]. As a consequence, selection should favour animals that are able to predict periods of favourable conditions to time life cycles such as reproduction or moult [38].

To our knowledge, this is the first experimental study demonstrating that a tropical organism can use the subtle celestial cue of the timing in sunrise and sunset to set its circannual clock. Because the annual variation in sunrise and sunset at the equator has previously been suggested to time the synchronicity in flowering and bud-breaking in tropical plants [12, 17], we suggest that the use of solar time may be widespread among taxonomic groups with strong seasonality within the tropics.

We thank Andrea Peter and Sonja Bauer for bird care and assistance with the measurements, and Monika Trappschuh for assistance with data entry. Furthermore, we thank Nicole Geberzahn, Michaela Hau and Alexander Schreuerlein for discussions and comments. This study was funded by the Max-Planck Gesellschaft, B.H. is supported by the European Social Fund in Baden-Württemberg. I.T.M. acknowledges support from NSF grant no. IOS-0545735. This paper is dedicated to the memory of the late Ebo Gwinner, who encouraged this kind of experiment in 1985 [31], and the famous chronobiology institute in Erling-Andechs.
REFERENCES