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Noisy clocks and silent sunrises: measurement methods of daily activity pattern

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Abstract

From insects to mammals, many animals engage in behaviours known to follow cyclic patterns over days (e.g. singing, diving or foraging behaviours). Many of them are regulated by external factors, such as light intensity, and are thus associated with sunrise, sunset or zenith. However, these astronomical events do not occur at the same time everyday: they vary with both the time of the year and the latitude. Logically, therefore, behaviour timing should be recorded relative to these events. Yet, in the field, recording the timing of behaviour is much less difficult with a clock, which is often deemed a suitable common proxy. In this paper, we assess the potential methodological problems associated with analyzing behaviours on the basis of clock time rather than with the actual position of the sun. To demonstrate the important difference between these methods of analysis, we first simulated a behaviour set at sunrise and compared the time of occurrence with the two methods. We then used a dataset, based on a long-term monitoring of hunting behaviour of African wild dogs, *Lycaon pictus*, to reveal how using clock time can result in erroneous assumptions about behaviour. Finally, we investigated the occurrence of sun time records in published field studies. As a majority of them did not take into account the relevance of astronomical events, it is probable that many result in faulty behavioural timings. The model presented can change clock-recorded time into actual deviation from astronomical events to assist current protocols as well as correct the already recorded datasets.

Introduction

Daily events are classically positioned in time with a clock on a 24-h period. The sun's position in the celestial sphere, recorded at the same 'time of day' (hereafter referred to as 'clock time'), changes on successive days throughout the year. These differences are due to the earth's tilt on its axis (23.5°) and its elliptical orbit around the sun. This change is plotted on what is known as an analemma.

Many studies of diel activities highlight the importance of the moment of the day in regulating animals' daily behavioural cycles (Aschoff, 1966; Daan & Aschoff, 1974; Boulos, Macchi & Terman, 1996; Semenov, Ramousse & Le Berre, 2000; Metcalfe & Steele, 2001). Numerous animal activities are likely to be a function of either light intensity or ambient temperature and thus of the sun's position in the sky: time of sunrise, zenith or sunset, or more generally 'sun time' rather than 'clock time'. Lunar events are also of biological importance. The 'clock time' of sunrises (zenith or sunsets, hereafter referred to as 'sun time') differs according to the latitude, longitude and date of the year. Consequently, observations of behaviours lasting months should take into account the variation of daylight length. In fact, patterns of behaviour may appear to differ if analyzed by clock time rather than by the deviation from sun time. Moreover, the tilt of the earth on its axis generates a difference in annual variation of sun time according to latitude. Consequently, the difference between clock time and sun time will be greater at high latitudes.

Although the difference between clock time and sun time is known, clock time is much easier to record when logging behaviours in the field. Consequently, clock time is often used in analysis rather than being converted to solar events. While the use of such a proxy for sun time may be justified for short-term studies close to the equator, where the difference is small, the increase of this difference with increasing duration and latitude has never been quantified.

We thus aimed at characterizing the potential error in recording behaviours with a clock, according to study duration and geographical location. The main goal of this work is to provide a simple tool for correcting the time at which behaviours are recorded when using a clock in order to make it corresponds to solar time. To highlight the importance of this, we first used a simple mathematical model to investigate the potential error of recording behaviours based on 'clock time', according to both the location and the duration of the study. We used the example of a simulated behaviour set at sunrise for ease of demonstration. We then used a real dataset, from a long-term study of the ecology of African wild dogs, *Lycaon pictus*, in Zimbabwe, to illustrate how using clock time rather than sun time may result in some artificial noise and thus to different conclusions regarding the observed behaviours. Moreover, we assessed the frequency of using a clock to record behaviours in published studies. We investigated 100 peer-reviewed papers studying various species and behaviours, lasting for different periods of time and located in a wide range of latitudes. Finally, we discuss the implication of this factor for the future collection of ethological, behavioural and demographic data as well as for the analysis of existing data.

Materials and methods

Modelling a behaviour set at sunrise

Determining the time of sunset (-rise) according to the date and latitude (Meeus, 1991; Meeus & Savoie, 1995; Savoie, 2001; and see Appendix S1) enables us to model an event occurring at sunrise (and recorded by clock time). Then, we intend to estimate the loss of information expressed as the noise due to change in sunrise while recording data using clock time.

We set a hypothetical behaviour occurring at sunrise. The demonstration holds for other moments of the day, such as zenith or sunset. For the sake of realism, the occurrence of this behaviour is not instantaneous, but rather follows a normal distribution centred on sunrise:

$$\phi_1(t) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(t-HS_{\text{rise}})^2}{2\sigma^2}} \qquad (1)$$

where ϕ_1 is the behaviour distribution during the day, t is the 'clock time', HS_{rise} is the clock time of sunrise and σ is the standard deviation associated with the distribution of the behaviour.

The density of probability reaches its maximum at HS_{rise}, meaning the best way to observe the behaviour is to watch the individuals at this time of the day. The probability density decreases symmetrically around its maximum, meaning the further one is from HS_{rise}, the less chance one has to observe the behaviour.

If a behaviour is to be observed daily over an N-day period, one can assess the overall distribution of the timing of the behaviour using either sun time or clock time.

The distribution of the behaviour as a function of the clock time after an N-day period follows:

$$\phi_2(t, N) = \frac{1}{N}\sum_{1}^{N} \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(t-HS_{\text{rise}})^2}{2\sigma^2}} \qquad (2)$$

Each day the distribution reaches its maximum at a different time (HS_{rise}, the sunrise time changes), so we expect the shape of the distribution to differ from that which would apply to a 1-day study. Consequently, the distribution is expected to flatten with the duration of the study. Hereafter, we will refer to this distribution, or method of collecting data, as 'clock time distribution', or 'clock time method'. However, the behaviour time could be recorded according to sun time, with $X = t - HS_{\text{rise}}$. Then, the distribution of the behaviour as a function of sun time after an N-day period still follows a normal distribution centred on 0 with variance σ^2. This distribution of the behaviour reflects the fact that each day the behavioural distribution is the same if the comparison time (referential) is the sunrise. Hereafter, we will refer to this distribution, or method of collecting data, as 'sun time distribution', or 'sun time method'. It is clear at this stage that the distribution ϕ_1 contains information about the timing of behaviour, while the distribution ϕ_2 also contains information about the change in sunrise time. We thus attempt to estimate the loss of information by quantifying the noise introduced by using ϕ_2 rather than ϕ_1.

To compare the 'sun time distribution' and the 'clock time distribution', we compute the ratio of maximum probability density for the two distributions. We will refer to it as the noise, or amount of information lost, ε:

$$\varepsilon = 1 - \frac{\text{Max}[\text{probability density from (2)}]}{\text{Max}[\text{probability density from (1)}]} \qquad (3)$$

equals zero when both distributions are the same (as in a 1-day study) and increases towards 1 as both distributions show differences.

Comparison of both methods using a real dataset (African wild dog hunting behaviour)

We illustrate this point using African wild dog data from Hwange (18-30S, 26-00E) over a 5-year time frame. Data were collected for all species throughout the year, with time of capture being recorded. Clock time obtained in the field was equated to the time of the appropriate solar event for the correct day, latitude and longitude using the National Aeronautics and Space Administration (NASA) almanac (see http://aa.usno.navy.mil/).

The behaviour we test is capture of major prey items in evenings: kudus (*Tragelaphus* sp.), duikers (*Cephalophus* sp.) and impalas (*Aepyceros melampus*). We test the behaviour time windows relative to sunset time as well as to clock time to see if the subsequent interpretations differ.

Literature research

We analyzed 100 papers (Appendix S2) related to behaviour and diel activity patterns. Those papers were found by searching for key words (i.e. 'diel activity', 'timing' and 'behaviour') on the '*web of knowledge*' search engine. They presented different ways of recording the time of the day, which led us to a classification of five different classes: (1) studies in laboratory environments with controlled 'Light and Dark' cycle (25

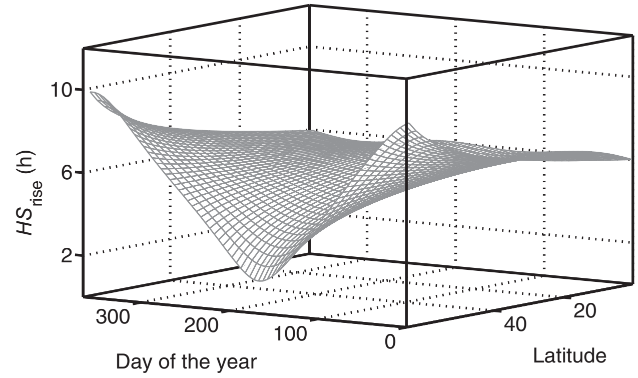

Figure 1 Time of sunrise, HS_{rise}, for different latitudes and throughout the year (see details in Appendix S1).

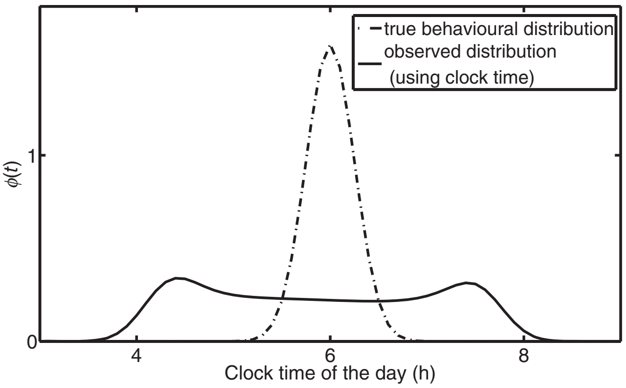

Figure 2 Distribution of a behaviour normally centred on sunrise (with $\sigma = 0.25$) recorded during 1 year at 45° latitude. Dashed line represents the distribution as a function of sunrise time (which conveys information about the behaviour timing only), while the solid line represents the distribution as a function of clock time (which conveys information about the behaviour timing, but with noise from the change in sunrise time).

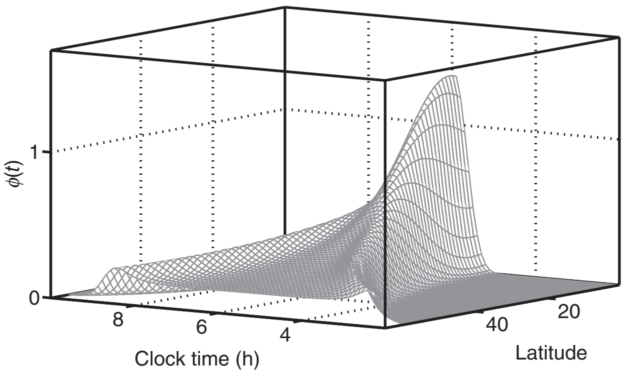

Figure 3 Distribution of behavioural activity, ϕ (t,L), as a function of 'clock time' over a year, for different latitudes (in degrees). The behaviour is set as a daily normal distribution at sunrise, with $\sigma = 0.25$. As latitude increases, the distribution is flattened, thus the real behaviour distribution is misrepresented due to increased noise, and much information is lost.

studies); (2) field studies using light intensity, time deviation from sunrise or sunset or sun angle rather than 'clock time' (25 studies); (3) field studies analyzing the time of behaviour using a monthly (or bimonthly) average of 'clock time' (13 studies); (4) field studies using a seasonal average of 'clock time' (9 studies); (5) field studies using 'clock time' (28 studies).

Using chi-square tests, we investigated the potential effect of study location and duration on the choice of methodology. Finally, we explored a potential difference in outcomes depending on the taxa being studied.

Results

Modelling a behaviour set at sunrise

Figure 1 represents the time of sunrise according to the date and latitude. These times reflect the interaction (see Appendix S1 for details) of the change both in time of sun crossing the meridian and in the hour angle (a measure of how high the sun is at midday). The variation induced in sunrise increases throughout the year with the latitude. We can also verify that shortly after 65° (when one reaches the polar circle at ±66°34′), both sunrise and sunset events happen at 12 (AM or PM). Thus, a 'day' of complete light or darkness occurs.

Using equations (1) and (2), it is possible to visualize the distribution of the modelled behaviour at any latitude and for any duration using either the 'clock time' or 'sun time' method. These distributions may differ greatly between both methods, especially for prolonged studies and at high latitudes.

Figure 2 illustrates this by presenting the resulting distributions after recording a behaviour for 1 year at 45° latitude using both methods. In particular, the expected distribution of behaviour as a function of 'sun time' is independent of the latitude and study duration. The expected distribution of behaviour as a function of 'clock time' might reveal more about changes in sunrise than about the actual timing of the behaviour.

We can then see the impact of the latitude by plotting the distribution of behaviour as a function of both 'clock time' and latitude (Fig. 3, equivalent to the solid curve in Fig. 2 for different latitudes). As expected, there is a general trend for the distribution to flatten at higher latitudes. It is clear from this graph that increasing the latitude will increase the amount of information loss, or noise, due to change in sunrise.

Finally, using equation (3), we estimated the information lost by using a clock time method rather than the more accurate sun time method. Figure 4 expresses the loss of information, or noise, according to the duration and the location of the study. We can observe that the noise increases as the latitude increases and as the standard deviation around sunrise decreases. The maximal amount of noise occurs when the study lasts for 6 months. Then, we observed a gradual gain

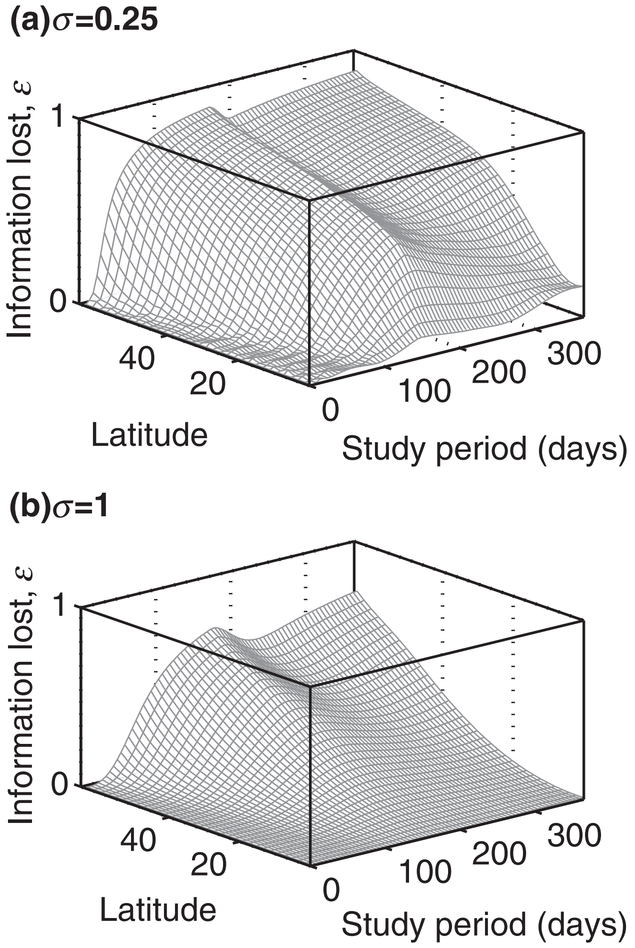

Figure 4 Percentage of information lost (ratio of maximum probability density between both methods), both as a function of latitude and duration, when clock time is used instead of sunrise time. Two behaviour occurrence distributions are used: about 95% of occurrences are included either (a) in 1-h period ($\sigma = 0.25$) or (b) in a 4-h period ($\sigma = 1$).

in information as the sunrise occurs at the same time as in previous days.

In conclusion, noise increases markedly with study duration and latitude. For instance, at 30° latitude, using clock time during a 6-month period, around 70% of the signal is lost due to noise (with $\sigma = 0.25$). The more spread the daily behavioural distribution (greater σ), the less noise results from using a ‘clock time’ method.

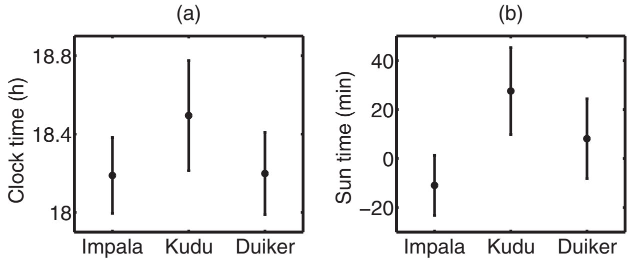

Figure 5 Mean time (and 95% confidence interval) of evening kill of three prey species hunted by African wild dogs, *Lycaon pictus*, according to records by clock (a) or by sun position (b). The differences between the two recording protocols reveal that the absence of behavioural differences observed for the hunt timing when clock time is used was, in fact, a recording artefact, which concealed the actual pattern of species-specific differences in kill timing, with kudu being killed later.

Comparison of both methods using a real dataset (African wild dog hunting behaviour)

Our comparison between behaviour time windows using both methods shows a significant difference in the obtained results: if the wrong method is used, the major prey items will be seen as being caught within the same time windows ($F_{2,165} = 2.17$, $P = 0.18$; see Fig. 5a). In reality (using deviation from sunset), we found significant differences in timing ($F_{2,165} = 7.34$, $P < 0.001$). In particular, kudus were captured significantly later than impala (Tukey's test, $P < 0.001$), showing a genuine prey selection related to hunt timing, which would have been overlooked using clock time. These results thus highlight that even at low latitudes (18°S), the truer significances will be lost in noise if clock rather than sun are used to measure event sequences.

Literature review

First, all controlled studies (i.e. as opposed to field studies) unsurprisingly indicate the exact variation in the daylight cycle. This may reflect and acknowledge the importance of light as a ‘zeitgeber’.

Among the field studies, only 33% used the actual variation of sunset and sunrise to characterize daily activity patterns. In contrast, 38% of field studies used clock time and finally 29% divided the study period monthly or seasonally, leading to difficulties of interpretation of the effect of change in the sun's position at a set clock time. Consequently, two-thirds of the ‘field’ studies we reviewed could be subject to misinterpretation caused by an inappropriate handling of time data. This is illustrated in Fig. 6, which accounts for the proportion of field studies that used the different measurement methods according to the latitude, duration of the study and taxa investigated.

Tropical studies are more likely to use ‘clock time’ probably because changes in sunrise and sunset are seemingly less marked there (χ^2, $P = 0.001$). Yet, two-thirds of the studies conducted between 30° and 60° used clock time (Fig. 6a).

The method used did not differ according to the duration of the study (χ^2, $P = 0.981$), despite the fact that long-term studies are more affected by the change in day length. In all cases, more than two-thirds of the studies failed to record time properly (Fig. 6b).

There was a trend for mammal and reptile studies to use the clock time more than studies of other taxa (χ^2, $P = 0.016$). Studies on reptiles, which are poikilothermic animals, would

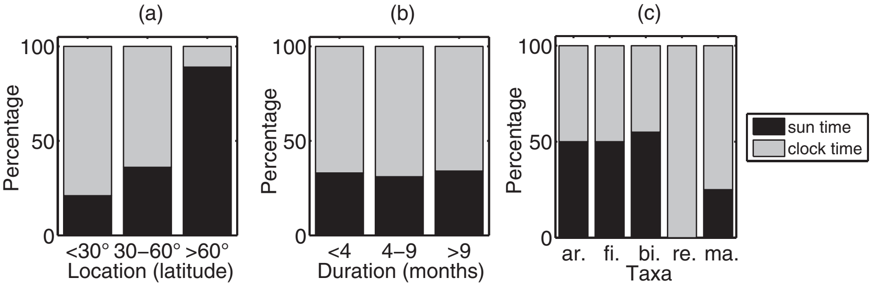

Figure 6 Percentage of field studies using either sun time or clock time to record behaviours, according to their latitudes (a), duration (b) or taxa (c). For the taxa subplot, the *X*-axis labels (ar., fi., bi., re. and ma.) stand for 'arthropods', 'fishes', 'reptiles', 'birds' and 'mammals', respectively.

be expected to take account for sun's position when recording time, but systematically used clock times (Fig. 6c).

This short review shows that even if the behaviour is recorded in high latitude, during a prolonged study and/or on poikilothermic taxa, a significant number of studies still use clock time, despite the risk of errors and misinterpretation due to changes in the sun's position.

Discussion

With a mathematical model based on astronomical parameters, we demonstrated that recording behavioural data in the field using the time given by a clock can generate substantial errors compared with the real time of events, as given by the position of the sun in the sky. These errors increase with both latitude and duration of the study.

The analysis of African wild dog hunting behaviour data shows that using clock time would have generated a false pattern, suggesting that all three prey species were killed within the same time windows. Sun time recording showed the existence of an actual pattern of species-specific time windows of prey kills, which differ in evening hunts and in which one species (kudu) is generally killed later than the others. This shows that significant noise can be generated by using clock time, even for studies undertaken in tropical regions.

Yet, our literature review revealed that a significant proportion of field studies of activity pattern took no account of the changes in astronomical events, especially at low latitudes. Where changes in sunrise or sunset time occur, and are likely to induce a switch in the timing of behaviour (e.g. at 30° latitude and higher, or lasting more than 4 months), a surprisingly large number of studies used clock time only. These may therefore have missed important insights. Studies presenting results by time period (monthly, seasonally) may partly circumvent the timing problem. However, this may confound changes in the animal behaviours and changes in environmental factors. Finally, studies of birds, mammals and reptiles seemed to be less mindful of these problems than those of fish and insects. This is especially surprising in the case of reptiles, for which no study was found to use sun time, despite reptiles being homoeothermic animals and thus highly dependent on the sun's presence for temperature regulation. While it might make sense to use temperature rather than time for cold-blooded animals, it would be even more logical for these animals to choose sun time over clock time if behaviours are to be associated with a time of the day cycle.

Variations of sunrise or sunset time have been known for thousands of years, and animal behaviour is known to follow such celestial events. First, it is well known that photoperiod works as a 'zeitgeber', regulating time of rest and activity (Boulos *et al*., 1996), leading to the emergence, five decades ago, of methods involving correcting clock time by sunrise and/or sunset time (Aschoff, 1954). Equally, it is noteworthy that due to the lunar clock not being synchronic with the solar clock, any study where the species is responding to lunar cues will be flawed if using noisy clocks. Second, it has been proven that in various taxa, general activity, as well as some very specific behaviour, is set on sunrise or sunset (Aschoff, 1966; Daan & Aschoff, 1974; Metcalfe, Fraser & Burns, 1999; Semenov *et al*., 2001). One could argue that for many (especially cold-blooded) species, temperature will be a better environmental cue to activity, but the temperature is often related to sun's position. Our point here is that the sun's position in the sky generally has an environmental meaning, whereas clock time has no biological or environmental meaning.

While it is apparent that it is important to use the most appropriate measure for behavioural studies, using sun time rather than clock time increases the complexity of data analysis; the important question is whether the increase in accuracy is warranted. The answer may differ with circumstance, as the duration and latitude of studies influence the relative pros and cons of different methods of time measurement.

Our intent here is obviously not to provide unconstructive criticism of previous behaviour studies, but rather to point to a more precise and meaningful method to record behaviours in time. We provide a simple model whereby behavioural data can be collected directly with clock hour and later on corrected to take into account temporal and geographical sun cycle variations. In addition, this model, available online (see Appendix S3 for a 'R' function to transform clock time data to deviation from sunrise (-set), also available online with potential update at http://www.ese.u-psud.fr/epc/conservation/pages/Franck/docs/SunTime.R), can be used to correct existing data and determine whether conclusions drawn using clock time need to be reworked.

Several possible caveats affect our model. First, the behaviour may not follow a normal curve. However, if maximum activity is set at sunrise, then the observed maximum activity will always decrease while looking at 'clock time' activity. Second, the model relies on some assumptions that make the time of sunrise imprecise. For example, we used an estimate of atmospheric refraction, which depends heavily on meteorological conditions, and we assumed that the horizon height was zero. However, these assumptions are generally unlikely to provoke errors of more than 1 or 2 min. Also, we have not modelled variation between countries that use a different time (1-h delay) between summer and winter. Finally, it is important to note that behaviour might be associated with other astronomical events than sunrise or sunset (e.g. full-moon, start or end of twilight) but could be equally corrected using the NASA almanac (see http://aa.usno.navy.mil/).

Many concepts of behavioural ecology and related fields rely on the regular recording of given behaviours during repeated periods. If those records, which are the basis of ensuing statistical analyses, were to be systematically flawed, the conclusion of many such studies would have to be re-evaluated. We provide here a simple method to do so, as well as arguments to make this correction to clock time-based datasets. We point out that the availability of this method allows the luxury of recording behaviours using a clock and later correcting the generated data into sun time correspondence. As the present methods makes it very easy to convert clock time into sun time (e.g. using Appendix S3) for either starting, ongoing or long-finished studies, behavioural scientists will be able to rely on unflawed data all the time.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of the references used in the literature review.

Appendix S2. List of the references used in the literature review.

Appendix S3. Code for a function in 'R' programming language that converts the clock time to sun time.