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REVIEW

A clock for all seasons in the subterranean

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Abstract

In 1976, Pittendrigh and Daan established a theoretical framework which has coordinated research on circadian clock entrainment and photoperiodism until today. The "wild clocks" approach, which concerns studying wild species in their natural habitats, has served to test their models, add new insights, and open new directions of research. Here, we review an integrated laboratory, field and modeling work conducted with subterranean rodents (*Ctenomys* sp.) living under an extreme pattern of natural daily light exposure. Tracking animal movement and light exposure with biologgers across seasons and performing laboratory experiments on running-wheel cages, we uncovered the mechanisms of day/night entrainment of the clock and of photoperiodic time measurement in this subterranean organism. We confirmed most of the features of Pittendrigh and Daan's models but highlighted the importance of integrating them with ecophysiological techniques, methodologies, and theories to get a full picture of the clock in the wild. This integration is essential to fully establish the importance of the temporal dimension in ecological studies and tackling relevant questions such as the role of the clock for all seasons in a changing planet.

Keywords Circadian clock · Entrainment · Photoperiodic time measurement · Subterranean rodents · Evening and morning oscillators · Wild clocks

Introduction

The cyclic movements of rotation and translation of the Earth have established the fundamental daily and annual time frames underlying biological phenomena. Much has been investigated on the endogenous nature and photic synchronization of daily and annual biological rhythms following the seminal, 1976 work of Pittendrigh and Daan. These authors synthesized experiments of behavioral responses to artificial light manipulation in four nocturnal rodents, shedding light on photic entrainment mechanisms and the role of the circadian clock in annual, photoperiodic phenomena.

Due to the central role of the light/dark cycle on the synchronization of both daily and seasonal phenomena, it was natural to speculate that the systems underlying these two modes of temporal organization had common elements. Interestingly, while several authors investigated whether the circadian clock located in the suprachiasmatic nuclei in mammals would be part of an unidentified circannual clock (Zucker et al. 1983; Dark et al. 1985), Pittendrigh and Daan pursued a distinct path, trying to understand how entrainment of the circadian clock could accommodate the day-to-day, annual variation of daylength (Pittendrigh and Daan 1976a, b, c). In other words, their seminal studies on the role of the circadian clock in photoperiodic phenomena focused on how the circadian clock participated in the input pathway of photoperiodic time measurement, as proposed by Bünning (1963) rather than on whether they participated in the production of seasonal rhythmicity. With this question in mind, they deepened into the realms of photic entrainment scrutinizing differences between nocturnal and diurnal organisms at the level of their Phase Response Curves (PRC) (Daan and Pittendrigh 1976a; Pittendrigh and Daan 1976b). Because the PRC establishes when organisms start their daily activity in relation to lights-on or off, they reasoned that intra- and inter-individual differences in the shape of PRCs could shed

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light on how their clocks compensated for annual daylength variation. A comparative study of these shape differences in four nocturnal rodent species was masterfully conducted, revealing functional inter-relationships between the value and stability of their free-running period, the PRC shape, range of entrainment, responses to different photoperiods, and to constant light conditions. More detailed exploration of the shapes of delay and advance areas of the PRC indicated a fundamental nocturnal entrainment strategy for conserving the phase angle between activity and darkness onsets (ψ), in face of the seasonally varying daylengths (Pittendrigh and Daan 1976b). However, to account for seasonally varying daily duration of activity (α), they transitioned masterfully from a one to a two-oscillator model of the circadian clock, proposing the Evening (E) and Morning (M) oscillators (Pittendrigh and Daan 1976c).

These studies established a theoretical framework that applies to all organisms and that has coordinated circadian system research until today. After decades since this work, several new insights have been gained through new approaches that spanned all levels of biological organization (Yoshikawa et al. 2017; Olde Engberink et al. 2020; Tackenberg et al. 2020). The objective of this review is to focus on how the “wild clocks” approach (Kronfeld-Schor et al. 2013; Schwartz et al. 2017), which concerns research using wild species in their natural habitats, has served to test Pittendrigh and Daan´s models and to add new insights. Extreme photic environments, such as the subterranean, caves, abyssal, or polar areas, can test the limits of laboratory-born models of entrainment (Beale et al. 2016). In particular, subterranean rodents have long been studied to verify persistence of rhythms and sensibility to light (Ben-Shlomo et al. 1995; Goldman et al. 1997; Oosthuizen and Bennett 2022) and technical advances have increasingly allowed studies under natural conditions (Sklíba et al. 2007; Vlasatá et al. 2017). Here, we review how our studies conducted with subterranean rodents in their natural habitats, combined with Lab experiments and mathematical modeling confirmed and translated Pittendrigh and Daan´s findings of daily photic entrainment and the “clock for all seasons” into the real world.

Synchronization of the circadian clock to the 24-h day/night has long been studied with model organisms under laboratory conditions, using artificially controlled light/dark (LD) cycles. In most cases, patterns of photic entrainment are studied under “rectangular” LD cycles comprising hours of continuous light and darkness. These simplifications of light/dark patterns have surprisingly worked well for entrainment and provided deep insights into synchronization mechanisms, but they indicated a long path toward translating this knowledge back to more realistic settings. De Coursey (1986) established the importance of rescuing the ecological perspective by adding semi-natural elements that retained the controllable condition of the lab but added more realistic light regimens than the rectangular cycles. She maintained flying squirrels (*Glaucomys volans*) in simulated den systems that allowed animals to expose voluntarily to light, aiming to achieve a more realistic mode of entrainment in the laboratory setting. In fact, their light-sampling patterns turned out to display more day-to-day variability, but entrainment could still be achieved and understood through their PRC. The strength of the PRC-based model of entrainment could also be associated with the fact that Pittendrigh and Daan investigated entrainment of nocturnal rodent species which were assumed to expose to light, in nature, during brief exposures in twilight times. This could be fairly well simulated by the T-cycles and skeleton photoperiods used in their lab experiments and whose resulting patterns could be explained by the PRC. On the other hand, decades later, Hut et al. (1999) released diurnal ground squirrels (*Spermophilus citellus*) into semi-natural enclosures carrying miniature light sensors. They verified that unlike nocturnal animals, these diurnal rodents did not expose to twilights at all, concentrating light exposure almost continuously during midday hours.

Following the steps of these pioneering works, our group developed a parallel lab, semi-field, and field study of South American subterranean rodents known as tuco-tucos. This desert species that we studied had its scientific name changed three times throughout the last 10 years: *Ctenomys* aff. *knighti*, *Ctenomys famosus* (Tammone et al. 2022) and now established as *Ctenomys coludo* (Sánchez et al. 2023). This species is neither social nor strictly solitary, showing an intermediate sociability level (Amaya et al. 2021). These rodents live underground in an extreme photic environment with no light, making studies of their temporal organization an opportunity to verify persistence of daily and annual rhythms as well as the limits of their photic synchronization. They displayed clear light-entrainable circadian rhythms in lab conditions (Valentinuzzi et al. 2009; Tachinardi et al. 2014; Yassumoto et al. 2019) and 24 h after-effects when transferred directly from field to lab DD conditions (Tomotani et al. 2012), indicating that they were robustly entrained in the wild. However, because they were rarely seen aboveground in the field, we hypothesized that their daily light exposure would be minimal. The “single pulse 24 h T-cycle”, extensively used by Pittendrigh and Daan (1976a), consists of one light pulse applied every day at the same time under lab conditions being the most simplified light regimen that can entrain the clock. This led us to hypothesize that tuco-tucos would emerge to the surface every day at a definite time, exposing to a mimicked single pulse T-cycle. However, visual observations of tuco-tucos released into enclosures revealed that they emerge to the surface several times during the day, apparently at random times, mainly to forage and to remove soil from their burrows (Tomotani et al. 2012) (Fig. 1A). To get more automated data of these patterns, we searched for light loggers that could be attached to their bodies to verify this hypothesis. Animal welfare indicate that external devices attached to animals should restrict to a maximum of 5% of their weight. Tuco-tucos (average 100–200 g) are much smaller than the ground squirrels (average 400–700 g) but the smallest light-logger developed at the time lied within the limits of what could be permissive for such animals. In this way, with these collared devices, measurements of tuco-tucos' daily light-exposure released into semi-field enclosures confirmed our previous observations and enabled development of computer simulations to test how such lighting patterns were able to entrain the clock (Flôres et al. 2016). The temporal pattern of their light-exposure did not resemble T-cycles at all due to the greater amount of emergence events per day, but, on the other hand, each emergence could fairly well be modeled by a light pulse, differing from the almost—continuous light—exposure of ground squirrels (Flôres et al. 2013). The temporal pattern of daily light-exposure of tuco-tucos promoted two immediate questions: how do these animals entrain their circadian clocks to 24 h through such irregularly spaced random light pulses and how could they measure daylength throughout the year?

The subterranean clock for day and night

Pittendrigh and Daan developed two models to help coordinate our understanding of photic entrainment, namely the "non-parametric" (discrete) and "parametric" (continuous) mechanisms of entrainment (Daan and Pittendrigh 1976b). The non-parametric model relies on the knowledge that a physical oscillator with period τ can be entrained by a cycle of discrete forcing pulses with period T, such as in a periodically kicked pendulum. These pulses cause abrupt phase-shifts on the oscillator, whose sizes and directions are phase-dependent, making the PRC the link between circadian studies and oscillator theory (Winfree 2001; Roenneberg et al. 2003). Synchronization explained by PRC is attained when each pulse causes a phase shift that corresponds exactly to the period difference ($T-\tau$) and a stable phase relationship ψ between the cycle of pulses and the oscillator is established. Entrainment to single pulse *T*-cycles and to two-pulse skeleton photoperiods are fairly well explained by the non-parametric model. On the other hand, the parametric model considers that light acts continuously on the clock whenever it is on. Daily entrainment is achieved by a continuous modulation of the velocity of the clock, accelerating or decelerating it to match the period differences ($T-\tau$) between its period and 24 h. This would resemble a pendulum continuously forced by a sinusoidal force which imposes its period *T*.

Considering entrainment in the real world, Pittendrigh and Daan (1976b) proposed that nocturnal animals could entrain basically via non-parametric entrainment assuming that they would expose to light during twilight times. Hut et al. (1999) proposed that, on the other hand, diurnal animals, which expose to light continuously during the day, would entrain through parametric mechanisms of light.

Computer simulations have consistently reproduced entrainment patterns of oscillators to single pulse *T*-cycles, as well as to rectangular or sinusoidal cycles, validating the non-parametric and parametric models of entrainment. More realistic light regimens require computer simulations

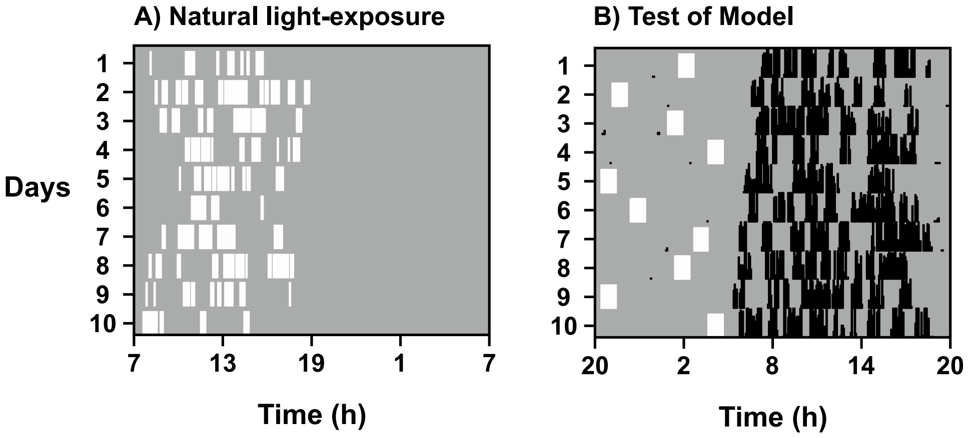

Fig. 1 Modeling daily light-exposure of tuco-tucos and experimental test of its efficacy as a zeitgeber. **a** Aboveground emergence times (white marks) of one individual animal in a semi-natural enclosure obtained by direct observation. **b** Experimental test of a daily single random light regimen. Entrainment is achieved by parametric and non-parametric features. The figure depicts the random dispersion of daily single light pulses (1 h; 1,000 lx) along a fixed interval I. The running-wheel activity of a representative tuco-tuco is represented by black marks. In both graphs, the horizontal axis represents time of the day and the vertical axis represent the number of days. Light exposure is marked in white over the darkness (gray) background (Modified from Flôres 2016)

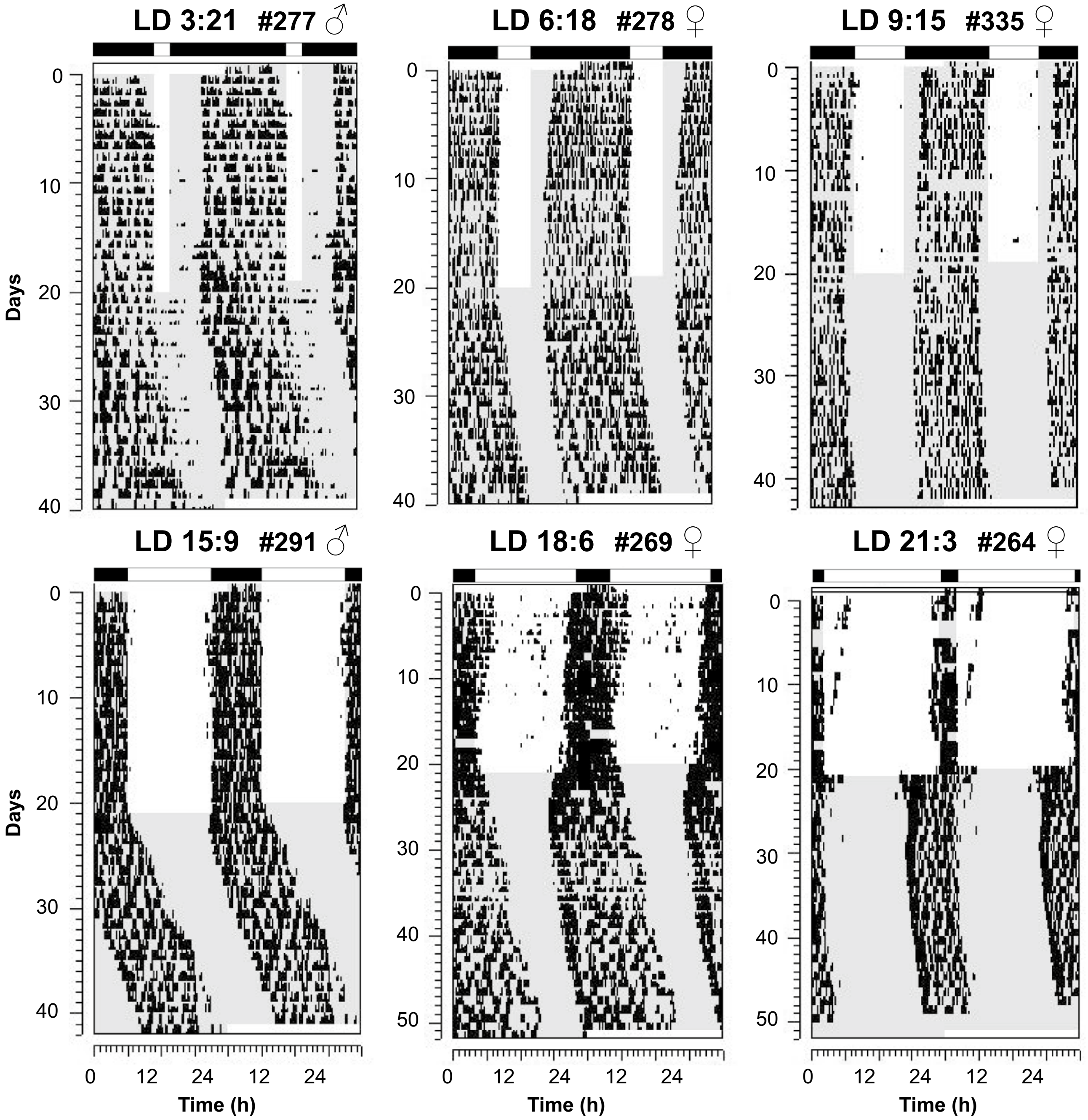

Fig. 2 Representative actograms of running-wheel activity of animals freshly caught from the field and submitted to different artificial photoperiods from extremely short (LD 3:21) to long days (LD 21:3). The light regimen is indicated by the LD bars (white for L phases and black for D) on top of each actogram as well as through the background colors in the body of the actograms (white represents the photophase while gray the dark phase). Animals were transferred from LD to DD on day 20. Animal ID and gender are indicated on the top right of each actogram. *LD* light/dark, *DD* constant darkness. Natural photoperiods on the days of capture, estimated from https://www.timeanddate.com/sun/@3865734: LD13:11 for #277, #278, #335; LD 14:10 for #299, #269, #264. (Modified from Improta et al. 2022)

that cover more complex scenarios (Schmal et al. 2020). We measured the PRC of tuco-tucos and verified that their time-dependent response to single light pulses was equal to the typical responses observed in other non-subterranean rodents (Flôres et al. 2013). To understand if a PRC-based entrainment could still be attained by their daily random light inputs, we modeled them focusing, first on the randomness of light pulse times. To this end, we first simplified the light regimen to a single 24 h T-cycle and added tiny random time deviations each day which did not break up entrainment. Then, the next step was to see how far we could deviate the time range of pulse deviation from the original *T*-cycle and still maintain entrainment. To our surprise, we achieved 24 h entrainment using single light pulses that could each day occur at any time of day within a range that went as far as 12 h (Flôres et al. 2013, 2018). This showed us that the single random light cycle was sufficient to entrain the circadian clock, extending the limits of photic entrainment to less predictable but nonetheless more realistic light regimens. We then captured tuco-tucos out of their natural burrows and tested our model of single random pulses inside wheel-running equipped cages. They confirmed the model by entraining fairly well to those most simplified light cycles (Flôres et al. 2016) (Fig. 1B).

Single random light pulse cycles entrain through both non-parametric and parametric mechanisms. While each light pulse causes a phase shift (non-parametric mode), each phase shift causes a slowly recovering amplitude change of the circadian clock, which is collectively translated into velocity changes that are the basis of the parametric mechanism. Figure 1B clearly shows that entrainment achieved by a regimen of single daily pulses—which essentially cause phase-shifts—does not result in abrupt phase changes with zigzag patterns as would be expected from a purely non-parametric response for random advancing and delaying pulses. Rather, the regular pattern results from slowly recovering amplitudes of the clock (Oda et al. 2000) which entail parametric velocity changes. In this sense, studies of wild species adapted to extreme photic environments reminded us that parametric and non-parametric mechanisms are models that help coordinate our understanding but need not be exclusive, especially in complex situations such as highlighted by the subterranean case.

The subterranean clock for all seasons

Our next question was whether and how subterranean animals could extract daylength information across seasons from the random nature of their daily light exposure.

Two conceptual models have been proposed for the mechanisms of photoperiodic time measurement, the “external” and the “internal” coincidence models, both having the circadian clock playing a central role. The external coincidence model of Bünning (1936) proposes that organisms discriminate long and short days through the detection of light occurring during a light-sensitive phase of the circadian clock. Under long days, light occurs during the sensitive phase while under the short days of winter light does not reach this phase. Alternatively, the internal coincidence model (Pittendrigh and Minis 1964) developed by Pittendrigh and Daan (1976c) proposes that different photoperiods change the internal conformation of the circadian clock, which is composed by at least two neuronal subpopulations. The (E) Evening and (M) Morning subpopulations of oscillators are mutually coupled but synchronized separately to dusk and dawn, respectively. As the timing of twilights change throughout the year, the phase relationship between E and M increases or decreases and so does the clock-controlled daily duration of activity (α). This could explain two features observed in natural conditions, namely the seasonal variation of daily duration of activity (α) (Daan and Aschoff 1975), as well as the seasonal conservation of ψ (Kenagy 1976).

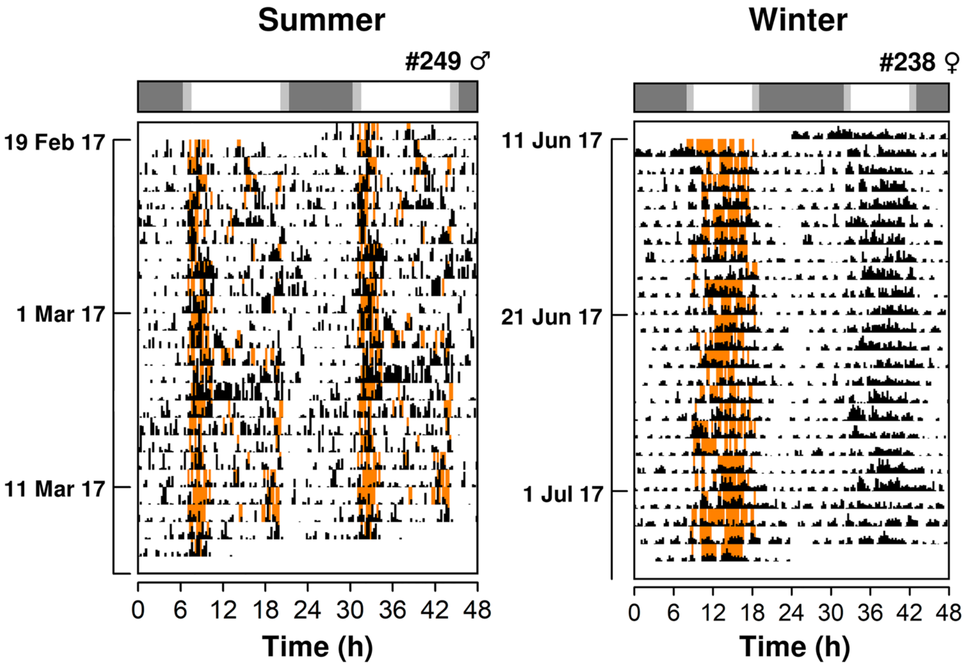

Fig. 3 Seasonal variation of daily light-exposure and activity rhythms. Double-plotted actograms of daily rhythms of gross motor activity and diurnal time on surface of two tuco-tucos kept inside individual field enclosures in Anillaco, La Rioja, Argentina, in the year 2017 during Summer (left) and winter (right). Orange marks: time on surface measured with collared light loggers during daylight hours. Black marks: gross motor activity measured with collared accelerometers. Bar above actograms: natural photoperiod at which each recording started (white: day; gray: night). Top right of each actogram: animal identification number and gender (from Jannetti 2018)

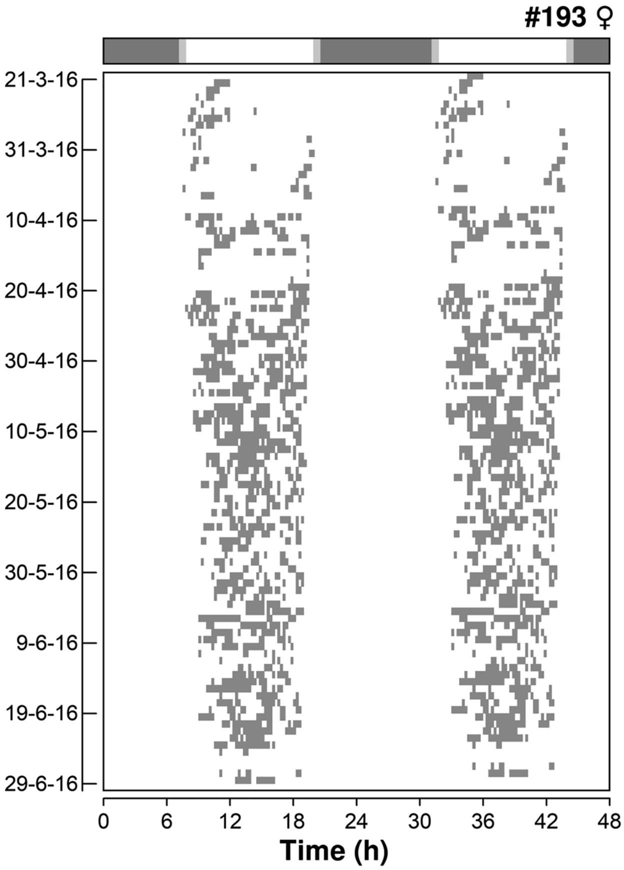

Fig. 4 Seasonal variation of daily voluntary surface activity and consequent exposure to natural light of a female tuco-tuco in open field during 3 months during the transition from summer in the South hemisphere to almost the beginning of winter. Gray marks: time on surface measured with collared light loggers that detect exposure to illuminance > 2 lx. Light and dark bars on top of the figure indicate natural photoperiod at the start date of registration (From Jannetti 2018)

Other downstream outputs of this photoperiod-dependent response of the clock, which were later confirmed, would be responsible for the complex seasonal changes in physiology (Ikegami and Yoshimura 2012; Nakane and Yoshimura 2019; Dardente et al. 2019).

Even though our studies indicated that the internal coincidence model accounts for the subterranean clock, several other factors also played important roles in the seasonal organization in the subterranean. To test if tuco-tucos were potentially able to detect different daylengths, they were exposed to artificial regimens ranging from extremely short to long photoperiods (LD 21:3, LD 18:6, LD 15:9, LD 9:15, LD 6:18 and LD 3:21) in the lab, spanning ranges much farther than those faced in nature (approx. LD 15:9 to 11:13 in the Argentinan region that they live, https://www.timeanddate.com/sun/@3865734). They changed their α and ψ (Improta et al. 2022) in a similar way presented by Pittendrigh and Daan in their experiments with non-subterranean rodents (Fig. 2). These results indicated that tuco-tucos were potentially responsive to different photoperiods. However, to fully understand how subterranean organisms measure daylength in nature, some crucial elements that are excluded from laboratory studies needed to be tackled: while tucos running on a wheel are forcefully exposed continuously to unescapable light regimens in lab cages, they expose to light as a result of their own behavior, in natural conditions. This is especially true in lab experiments of artificially varying photoperiods, where animals are continuously submitted to different daylengths, while their activity parameters are registered (Improta et al. 2022) (Fig. 2). In nature, they expose to long or short days voluntarily and we had already seen that they emerge to light in brief and random episodes.

To test if tuco-tucos in nature nevertheless are detecting and responding to photoperiod variations, they were first captured in summer and winter and released immediately into lab DD. Their summer and winter free-running activity rhythms clearly displayed different α, which are the imprinting of photoperiod after-effects (Tackenberg et al. 2020; Improta et al. 2022). This result showed that they were processing photoperiodic time information under field conditions (Flôres et al. 2021). Our next step was to understand how they achieved this.

Tuco-tucos were released into semi-field enclosures not only carrying light loggers but also accelerometers (as used by Williams et al. 2014; 2016) for long-term monitoring, to verify how their daily light-exposure patterns and locomotor activity changed throughout the seasons. Biologging devices revealed very interesting seasonal changes in both rhythms. Light-loggers—which detect aboveground activity—revealed that the daily pattern of light exposure changed with the seasons: while they concentrated their random exposure during middays in winter (Jannetti et al. 2019), they exposed to light mostly during twilight hours during summer (Flôres et al. 2021) (Figs. 3, 4). These results showed that through their own voluntary behavior, they exposed to different daylengths which, in turn, resulted in seasonal variation of photoperiod exposure. These results lead us to the question of which factors drive these animals to emerge to the surface in seasonally different times in nature, resulting in exposure to short and long days?

Two factors, endogenous and exogenous, drive tuco-tucos to emerge to the surface and see light at different times of the day across seasons. The endogenous component was highlighted by our accelerometer data which indicated that the clock-controlled daily activity maintains ψ but changes α throughout the year (Flôres et al. 2021). This could be interpreted by the internal coincidence model of Pittendrigh and Daan provided that the circadian clock of tuco-tucos is composed by coupled E and M oscillators (Valentinuzzi

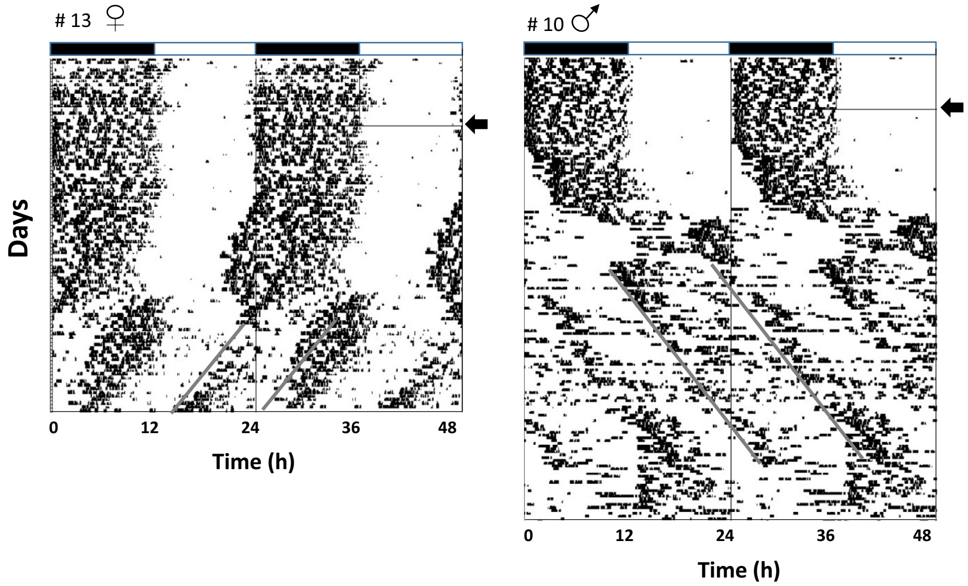

Fig. 5 Double-plotted actograms of two of the many animals that showed splitting when submitted to constant light. Time is plotted across the horizontal axis (48 h per line), and successive days are plotted beneath one another. The bar on the top indicates the light–dark cycle during the first days under LD condition; triangles on the right indicate start of constant light condition. Lines through onsets help visualize the periods of the splitted components during the constant light condition: last 50 days (left actogram) and during 60 days (right actogram). Top left of each actogram: animal identification number and gender (Modified from Valentinuzzi et al. 2009)

et al. 2009; Flôres et al. 2021) (Fig. 5). In this sense, accelerometer data indicate that long- and short-day photoperiods shape the clock-driven activity of tuco-tucos making them active underground for shorter or longer *α* durations of the day. The next step was to understand the exogenous factor which drives these animals to emerge to the surface at the extreme twilight times of long days in summer or at middays in winter, resulting in different photoperiod exposure.

The exogenous component shaping the activity of tuco-tucos was verified through ecophysiological statistical modeling that showed that emergence times are significantly associated to ambient temperature (Flôres et al. 2021). Studies in non-subterranean rodents had shown before that they avoid being active during the hottest hours of the day in summer, restricting activity at twilight times and prefer being active in the warmest hours of midday in winter (Kenagy et al. 2002; Rezende et al. 2003). In the case of subterranean rodents, we verified that additionally, the underground temperature plays an important role especially in winter. This is due to the time delay between surface and underground temperature, which can attain 12 h difference in winter (Jannetti et al. 2019). In this sense, tuco-tucos tend to emerge to the surface during midday when it is coldest underground and warmest on surface, while they emerge during twilights in summer to avoid the surface heat load of midday. In sum, ambient temperature shapes the seasonal change in the timing of surface emergence in tuco-tucos, which results in exposure to long days in summer and short days in winter. This differential exposure to seasonal photoperiod in turn shapes the circadian clock to extend activity time in summer and shorten it in winter, further increasing the probability of surface emergence at those different times, closing the loop. In sum, while wheel-running tuco-tucos measure daylength in the lab under constant temperature and continuous exposure to LD cycle, they achieve daylength measurement in nature by voluntarily leaving the tunnel to surface and exposing to light at different times of the day, which are in part shaped by varying ambient temperature and in part by their endogenous clock.

As a final step, we performed explicit computer simulations of Pittendrigh and Daan´s conceptual model of internal coincidence. We wanted to verify if skeleton photoperiods were really able to differentially entrain E and M oscillators and produce the experimentally observed changes in activity onset and α variations. This system was depicted as a two-zeitgeber model (Oda and Friesen 2011) using each light pulse of the skeleton photoperiod as a distinct zeitgeber. Our simulations confirmed and indicated the minimal two-oscillator configuration which were necessary and sufficient to replicate the experimental findings (Flôres et al. 2020). We then asked whether the random light exposure of tuco-tucos would be able to differentially entrain E and M (Fig. 6). To this end, we added randomness to the timing of the two daily light pulses that comprised the skeleton photoperiods and verified that when we changed the range of these random pulses, they were still able to differentially entrain E and M and cause the observed seasonal changes in α (Flôres et al. 2021).

Laboratory and field studies

By the same time Pittendrigh and Daan´s seminal works were conducted in strictly controlled laboratory conditions, Patricia de Coursey called attention to the ecological counterparts of entrainment models, adding several semi-natural elements to laboratory studies. The wild-clock approach

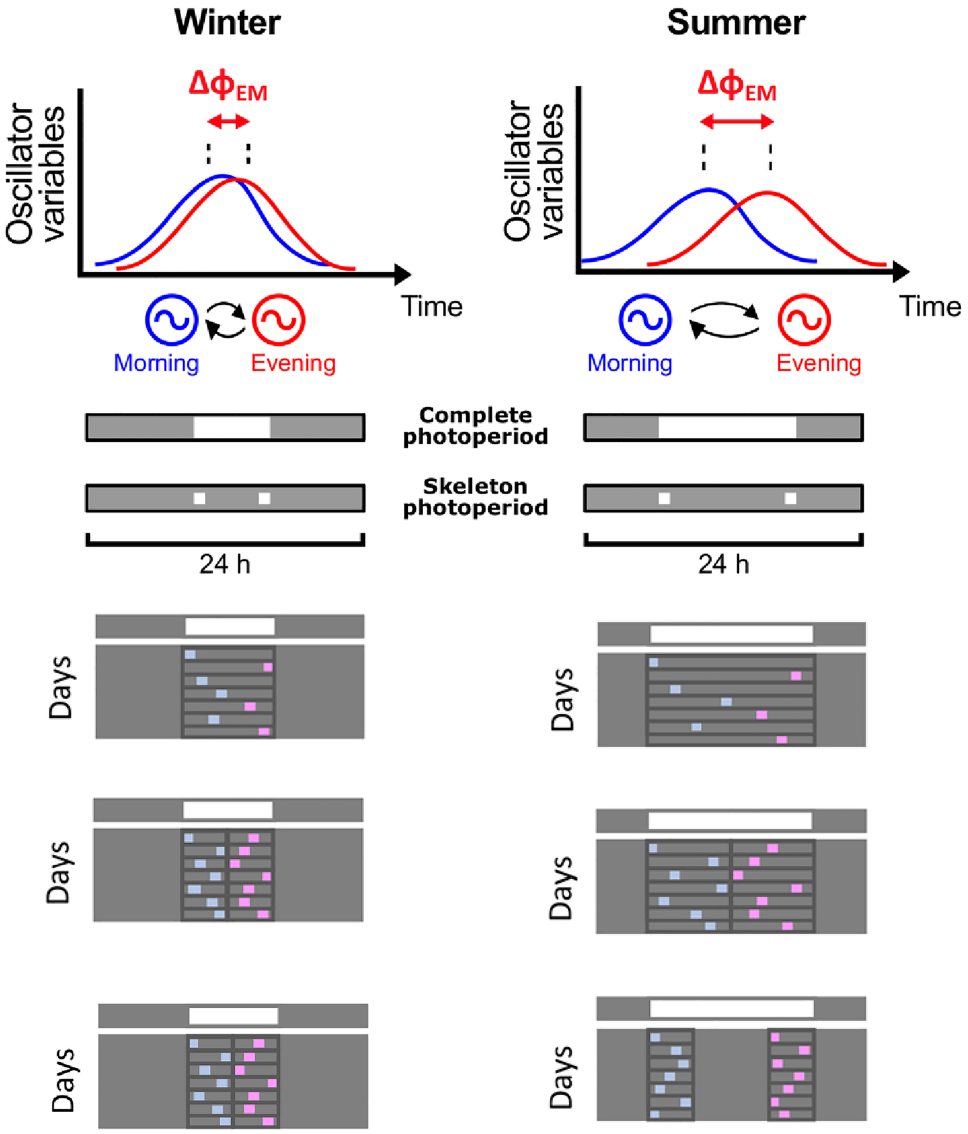

Fig. 6 Schematic representation of the two-oscillator model of the circadian clock and its role in photoperiod encoding. The model proposed by Pittendrigh and Daan (1976c) consists of a morning (M) oscillator that tracks dawn and an evening (E) oscillator that tracks dusk. M and E (circles) are coupled to each other (curved arrows). In the upper graphs, blue and red curves represent the state variables of M and E, respectively. As the photoperiod changes from short days in winter to long days in summer, there is a change in the phase relationship between E and M ($\Delta\Phi$, red horizontal arrows), which modifies the state of the circadian clock. Below the graphs, gray/white bars represent the light/dark times of the LD cycles. Upper bars indicate an LD cycle with complete photoperiod, i.e., light occurring during the complete photophase. Lower bars represent skeleton photoperiods, a simplified experimental protocol that reproduces the effects of photoperiod with only two light pulses, applied at the twilights. A mathematical model was used to simulate three scenarios of light exposure at different seasons (Models 1–3, in winter and summer photoperiods), and their impact on the synchronization of a two-oscillator model of the circadian clock. M and E oscillators, mutually coupled, were exposed to daily light pulses at random times within the photophase. Pulses between light onset and midday were applied to M (blue squares), and pulses from midday to light offset were applied to E (pink squares). Lines around the light pulses on each day delimit the distribution interval of the pulses. For details on the light exposure models, see Flôres et al. (2021) (Modified from Flôres et al. 2021)

benefitted greatly from technological advances enabling long-term and automated tracking of animals in their natural environment (Williams et al. 2014; 2016; Dominoni et al. 2017; Silvério and Tachinardi 2020). This approach allowed testing and confirming several aspects of Pittendrigh and Daan´s daily photic entrainment and the internal coincidence model behind the clock for all seasons. While transitioning from the lab to the field, we could pinpoint at least three elements that had not been considered in Pittendrigh and Daan´s models of entrainment and which offers plenty of study opportunities:

(a) The feedback of output rhythms on the clock: The circadian system is formally depicted as a linear sequence of zeitgeber input pathways, the circadian oscillator and several output pathways (Roenneberg and Merrow 2005). While laboratory experiments which impose lighting regimens are literally based on this model, field studies highlight the importance of the feedback of output rhythms on the clock itself, closing the loop of the linear zeitgeber-clock-output model. Subterranean rodents called attention on the voluntary nature of light exposure and how the resulting time of light input depends on the output activity time. The same idea applies to more complex scenarios of translational research such as those involving human natural photic (Wright et al. 2013) and food entrainment, because the timing of food input depends primarily on that of output eating behavior (Kaczmarek et al. 2017; Zhang et al. 2023). Furthermore, still on translational research, several studies go deeper on the complexity of the circadian system, focusing on how activity per se, translated into exercise, feed-backs on the timing and stabilization of the clock itself (Reebs and Mrosovsky 1989; Buijs and Escobar 2007; Leise et al. 2013).

(b) Masking of daily rhythms by environmental factors: While Pittendrigh and Daan´s studies focused on the clock-controlled, endogenous factors that shape activity rhythms, it has long been known that exogenous factors, including light itself, can in parallel mask the amplitude of output rhythms (Aschoff 1960). Masking was apparently ignored throughout their seminal work, but we conjecture that perhaps it was the reason for the absence of extremely long-day photoperiods in the graphical depictions of photoperiod-dependent ψ (Pittendrigh and Daan 1976b). In our experiments of tuco-tucos under artificial photoperiods, all animals were released into DD at the end of the protocol (Fig. 2). For those individuals exposed to extremely long-day photoperiods, ψ could only be deduced from the time of activity onset at the first days in DD, because they were clearly masked under LD but reliable under DD due to the after-effects of entrainment. More interesting than that was the challenge of identifying masking under field conditions. While there are several protocols that allow identification of masking factors in lab experiments by isolating the effects of each factor, it is extremely complex to do it with field data due to the simultaneous occurrence of all masking factors. In the field, even the decision of where to fix the thermometer is far more complex than the simplicity of attaching it on any wall inside the lab (as described in the legend of Fig. 7, for instance). To identify the masking factors that shape activity rhythms in the wild, we need to rely on sophisticated statistical modeling commonly used in ecophysiology studies that rank the factors that significantly inhibit or stimulate the behaviors under study (Long et al. 2005; Jannetti et al. 2019; Flôres et al. 2021) (Fig. 7). However, these often ignore the time of day and the endogenous component of biological rhythmicity. In this sense, a better integration is needed to get a full picture of the factors that shape activity patterns in nature: ecophysiological methodologies for identifying exogenous factors and chronobiological protocols for identifying endogenous factors (Halle and Stenseth 2000; Kronfeld-Schor et al. 2013; Schwartz et al. 2017). Our wild-clock study on subterranean rodents showed the simultaneous action of the circadian clock and of temperature masking in shaping activity patterns, highlighting the importance of integrating interdisciplinary approaches.

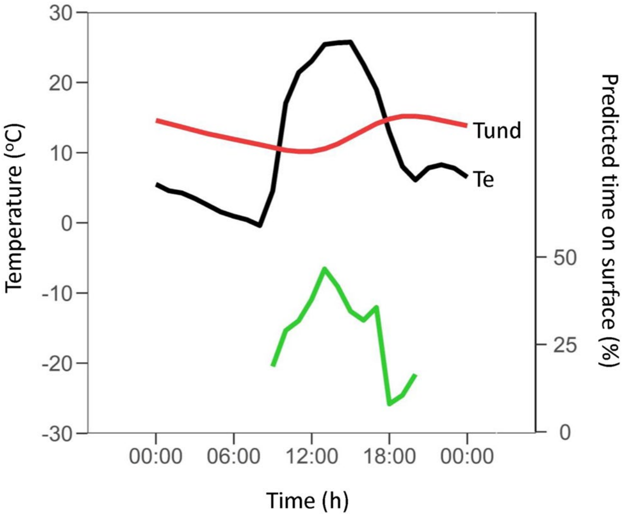

Fig. 7 Prediction of a generalized linear model of tuco-tucos' time on surface in response to environmental temperature factors. This prediction was constructed with time of day, Te (operative temperature, as measured with a temperature sensor placed inside a taxidermied tuco-tuco maintained for many days in a selected spot of their natural habitat and exposed daily directly to the meteorological conditions. The preserved skin was secured/mounted over an internal form (mannequin), and arranged in a life-like pose), Tund (20 cm underground temperature obtained with buried sensors) and Wind values of an arbitrary day during winter (15 July 2016), in Anillaco, La Rioja, Argentina. Green line: predicted time on surface; black line: Te; red line: Tund. Wind speed variation was omitted for better clarity (From Jannetti et al. 2019.). Bünning E (1936) Die endonomen Tagesrhythmen als Grundlage der photoperiodischen Reaktion. Ber Dtsch Bot Ges 54:590–617

(c) The unsolved mechanism behind nocturnal/diurnal definition.

Responses of dark- and light-active animals to manipulations of artificial light–dark cycles in the lab provided

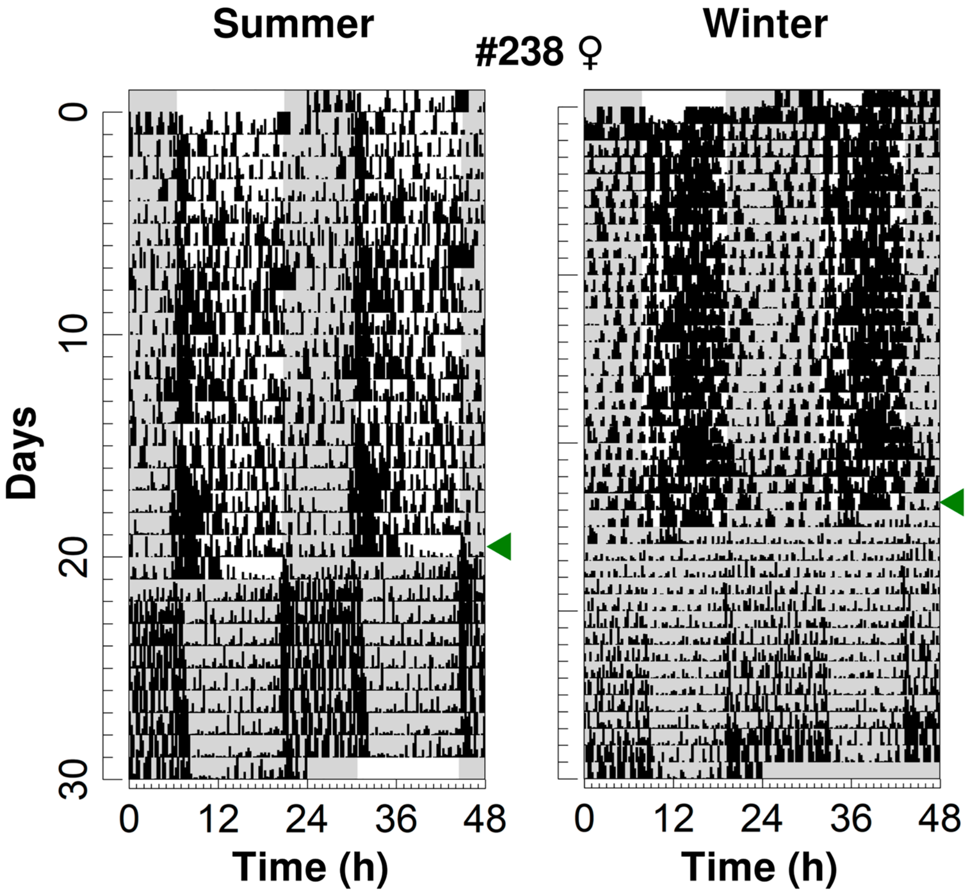

Fig. 8 Diurnal activity in the field and activity during subjective night in constant conditions in the lab. Activity time is defined downstream from the clock, while onset-to-offset transition times are dictated by photoperiod entrained clock. Double-plotted actogram of daily rhythms of gross motor activity of one female tuco-tuco (#238) kept inside field enclosures during summer (left) and winter (right) and then released into constant darkness in the lab. Black marks: gross motor activity measured with accelerometers. Bar above actograms: natural photoperiod at which each recording started in the field (white: day; gray: night). Arrows indicate day of transference. Top left of the figure: animal identification and gender (Modified from Jannetti et al. 2023)

the first insights toward the far more complex issue of nocturnalism and diurnalism in nature. Pittendrigh and Daan (1976b) assumed that diurnality and nocturnality were defined at the level of the clock and they searched for differences in their PRCs. However, more ecologically oriented studies (Halle and Stenseth 2000) contrasting laboratory and field conditions along with the gained knowledge on the anatomical basis of the circadian system (Yan et al. 2020) have indicated, with increasing evidence, that the diurnal/nocturnal determination in nature may occur downstream from the circadian oscillator and that this determination presents far more plasticity than originally suspected. One of the main indications that the definition of nocturnal/diurnal activity occurs downstream the clock comes from experiments where animals are transferred from field to laboratory DD. When tucos are maintained under lab LD and then released into lab DD, they display nocturnal activity, after-effects of previous entrainment and then free-run during subjective night, from the phase dictated by the clock (Valentinuzzi et al. 2009). When transferred from the field, despite the diurnal activity presented there, we see under DD the same aftereffect and free-running activity in subjective night without transients, showing that the clock did not change its phase during the field-to-lab transition and that the field diurnal activity was not dictated by the clock (Levy et al. 2007; Tomotani et al. 2012; Jannetti et al. 2019) (Fig. 8). The mechanism behind the diurnal/nocturnal switch between field and lab is still unsolved, but several works have indicated that discrepant energy requirements may be an important factor (Hut et al. 2012; Tachinardi et al. 2015, 2017; Van der Vinne et al. 2015). Our study using accelerometers, which register activity both in field and lab conditions confirmed unequivocally that tuco-tucos are dark-active in the lab but diurnal in the field and this was shown also for body temperature rhythm (Jannetti et al. 2023). It has been demonstrated that a threshold level of electrophysiological activity in the SCN defines the switch time between rest and activity (Houben et al. 2009). Interestingly, our studies highlighted that the clock does in fact define this switch- time but does not determine, within this timeframe, whether the animal is diurnal or nocturnal. This was shown dramatically by our field/lab transfer experiments where activity-on switched to activity-off immediately (Fig. 8). A diurnal animal became nocturnal instantly but the timeframe did not change. Interestingly, this was also true when comparing lab/field activity in summer and winter:

while their activity α is shorter and longer, respectively, under long and short artificial photoperiods in the lab, the inverse is displayed after the switch in the lab. Furthermore, this switch occurs by activity onset switching to offset, without change in phase (Fig. 8). Whichever the mechanism behind these flexible activity time switches, the timeframe established by the entrained clock is rigid, as emphasized by Pittendrigh and Daan. And this timeframe changes with photoperiod, being functional across seasons.

Macro-ecology studies based on field populational activity patterns have been increasing due to the development of new animal tracking technologies. While most studies of the effects of global climate change are focusing on changes in space distributions, such as migrations between latitudes or altitudes, there are increasing evidence that temporal changes have also occurred in some species and environments, with diurnal animals finding refuge from heat load or from new predators during the night (Gaynor et al. 2018; Calebe 2020). Additionally, changes in seasonal patterns have also been verified in populational activities, associated to global warming (Chmura et al. 2023). While most of these changes have been interpreted by ecophysiologists exclusively as acute reactions to new external factors, chronobiologists need to clarify the endogenous mechanisms at the individual level determining the time of output activity. This will enable us to understand if and how much the clock for all seasons can accommodate climate alterations in a changing planet.

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Data availability Data is available upon request.

Declarations

Conflict of interest The authors declare no competing interests.

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