Schwartz, W. J., Helm, B. and Gerkema, M. P. (2017) Wild clocks: preface and glossary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1734), 20170211. (doi:10.1098/rstb.2017.0211)

Wild Clocks

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The critical significance of biological timing and timekeeping is well appreciated by both chronobiologists and ecologists, and historically the two fields were linked early on (for example, see Enright 1970; Daan & Aschoff 1982; Dunlap et al. 2004). Sixty years ago, a diagram appeared in a book of papers from the 15th Symposium for the Study of Development and Growth (Figure 1; Pittendrigh and Bruce, 1957) that set the stage for future research on biological time. This schematic – with daily rhythmicity generated by a "clock" composed of one or more "endogenous self-sustained oscillators" (ESSOs) entrained by 24-h rhythms of light and temperature – became a blueprint for research by many chronobiologists on the mechanisms of internal timekeeping within organisms. Since then, our mechanistic understanding of daily and annual timing has blossomed, now encompassing details at the molecular, cellular, tissue, and organismal levels. The 1957 figure also included an input from "residual periodic variables" (RPVs); these were meant to represent abiotic factors such as "pressure, humidity, air ionization, cosmic ray showers" (Pittendrigh and Bruce, 1957) but could also pertain to biotic factors such as food availability, predators, competitors, and mating opportunities. Since then, ecologists have demonstrated the importance of daily and annual timing for individual fitness, with deviations from optimal timing possibly resulting in reduced foraging success, survival, and reproductive output.

To some extent, over the next decades the research programs of the two fields became non-overlapping, with chronobiologists focusing on unraveling the endogenous clock machinery and ecologists addressing the functional significance of timing in nature. Both by necessity and design, mechanistic work mostly has been conducted using a limited number of model organisms, each living in isolation, housed under standard (and, except for the rhythmic alternation of light and darkness, unchanging) conditions, with food ad libitum. Clearly, a successful life in the laboratory does not translate to survival in the wild. For chronobiologists to understand the significance, function, and evolution of endogenous clocks, they must turn to richer natural environment(s), where abiotic and biotic factors impose significant adaptive challenges that are integral to a species' ecological niche. Conversely, ecologists often have not considered the profound innate temporal programming that organisms undergo, including rhythmic changes in gene expression and physiological capacity, that regulates their responses to diverse perturbations. This persistent dichotomy has even led some authors to lament that there is an "…almost insurmountable gap between [the two groups], who seldom, if ever, are aware of each other" (Halle & Stenseth 2000).

The time is now ripe to reinvigorate a truly synthetic approach. We now have at hand: tools to record, analyze, and even manipulate gears of the endogenous oscillatory machinery; identified markers of the multimodal outputs of brain and body clocks; and new and powerful devices and analytics for tracking animals and their physiological indices in the wild, both over space and time. This issue, inspired by a meeting of chronobiologists and ecologists at the Royal Netherlands Institute for Sea Research on the island of Texel in the Netherlands ("Wild Clocks: Ecology Meets Chronobiology," March 15 to 20, 2015) seeks to catalyze such a reunification, highlighting new advances and approaches that can address the interdependence of chronobiology and ecology. In the following eleven papers, we assess where the intertwined fields stand in connecting functional and causal principles, in an evolutionary perspective.

The first article lays a foundation by assessing the concepts and assumptions with which ecological and chronobiological researchers approach biological timekeeping. The main finding is that the two fields share a deep interest in consistent temporal phenotypes (chronotypes) and in phenotypic plasticity of timekeeping, which offer a basis for future integration (Helm et al., this issue). Subsequently, two articles highlight the exciting new tools that now provide major advances in both fields. The first gives an overview and several case studies of new technologies for field research on timing in wild animals (Dominoni et al., this issue). The second details the power of new technology for research on sleep. Because physiological methods can now be taken afield, exciting new answers to old questions about the function and evolution of sleep may be within reach (Rattenborg et al., this issue). With new tools and a better understanding of clocks, differences in findings from studies in the field and the laboratory can now be approached as indicators of flexibility of biological timekeeping. The next article examines such differences and their mechanistic basis. It highlights how peripheral tissue clocks, for example relating to endocrine, metabolic and reproductive processes, contribute to the flexibility that is required of functional timekeeping in natural environments (van der Veen et al., this issue).

The three following contributions apply the strengths of integrated chronobiological and ecological approaches to key topics of seasonal biology. These include resource use in mammalian and avian reproduction, annual alternation between rest and active phases of insects, and seasonal migration of birds. The three articles identify timing programmes and their roles, respectively, in the capital-income-breeder spectrum (Williams et al., this issue), in timely activation from diapause and other insect life-cycle stages (Denlinger et al., this issue), and in enabling migratory species to exploit geographically distant resource pulses (Åkesson et al., this issue). These reviews are followed by an in-depth look at intra-specific variation in timing from an evolutionary stand-point. Selection in the wild for biological clocks is poorly understood, and even less so are possible contributions of sexual selection, which the article takes as its focal point (Hau et al., this issue).

The final three contributions examine interspecific dimensions of biological timekeeping. The stage is set by an overview article which emphasizes that fitness implications of biological clocks depend on species interactions, e.g., in contexts of food availability, predation, or parasitism (Kronfeld-Schor et al., this issue). Then, the importance of such interactions is highlighted based on an exemplary system, the finely timed co-evolution between flowering plants and their pollinators, which ultimately affects species interactions up to community levels (Bloch et al., this issue). Interspecific interactions reach their possibly highest temporal complexity in marine environments, which in addition to daily and annual rhythms are also subject to substantial fluctuations at tidal and lunar time scales. The closing article in this collection reviews knowledge of the temporal multi-tasking that is required in these environments, and the burgeoning insights into how several simultaneous clocks tick alongside each other in a single organism (Bulla et al., this issue).

A new chronobiological / ecological rapprochement is not only exciting but particularly urgent, given evidence for the increasing levels of light at night and progressive climate change, raising critical questions about disruptive effects on biological timekeeping. The resulting shifts in ecological balance, still incompletely understood, could eventually lead to reduced biodiversity and ecosystem instability (Hölker et al. 2010; Stevenson et al. 2015). The search for answers, including some that will come from the construction and curation of large temporal datasets partly collected and analysed through citizen science approaches, demands an integrated causal and functional approach.

We thank the Koninklijke Nederlandse Akademie van Wetenschappen (KNAW) and Rijksuniversiteit Groningen (RuG/FWN Center for entrepreneurship) for financial support for “Wild Clocks,” and Ms. Helen Eaton for invaluable editorial assistance.

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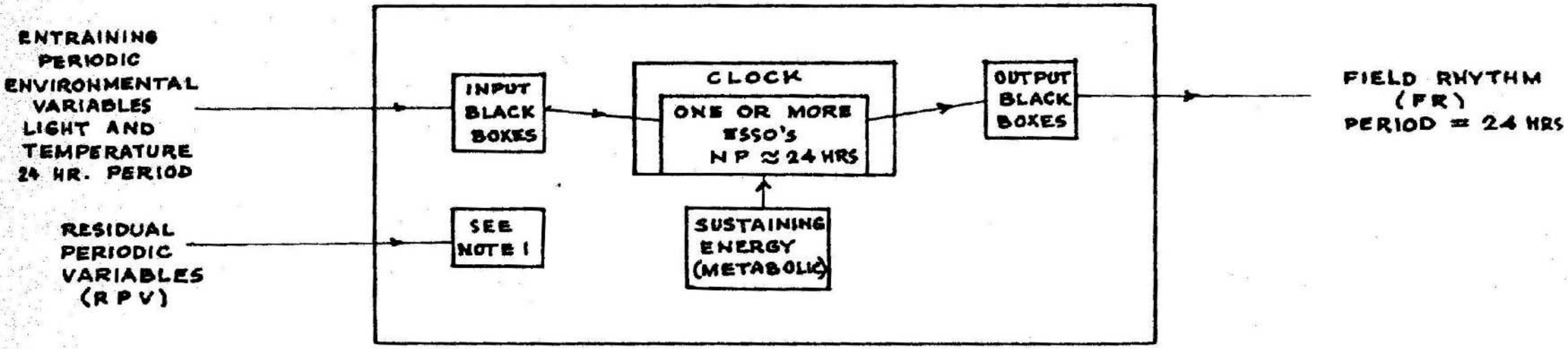


A - BLOCK DIAGRAM OF AN ENTRAINED FIELD RHYTHM (FR)

Glossary: definitions of key terms

Abiotic time: All aspects of geophysical cycles and their predictable consequences, including the duration and intensity of light exposure, cycles in temperature, humidity, precipitation and gravitation (note that effects of some of these factors can be modified by an organism's own behaviour; e.g., hiding underground).

Amplitude: Difference between the maximum or minimum value of a behavioural or physiological rhythm and its mean (level).

Biotic time: All aspects of the living environment that affect an organism's specific biological or physiological rhythm, including the influences of conspecifics (social interactions), competitors, predators and prey.

Chronotype: Characterisation of consistent timing (phase) of an individual's entrained behavioural or physiological rhythm. It relates phase markers of a rhythm of choice (e.g., activity), or the composite of an individual's rhythms, to an external phase-reference (e.g., midday) and to other individuals measured under similar conditions (eg., early vs. late types). An example is wake-time relative to sunrise.

Effector systems: The organ systems (e.g., muscles or exocrine glands) of the animal body which mediate the influence of the central nervous system on overt behaviour such as movement or secretion.

Endogenous rhythm: A rhythm capable of self-sustained oscillations, generated by living organisms without need for external rhythmic input (i.e., periodic repetitions are generated under constant environmental conditions).

Entrainment: The process of synchronization of the clock's oscillation to the *Zeitgeber* (usually the environmental day-night cycle) by resetting clock speed and/or phase.

External time: The time measured conventionally as clock time at a given location, measured from midnight (=0) until midnight the following day [1].

Free-running rhythm: The endogenous rhythm exhibited under constant conditions, characterised by its period length and amplitude.

Internal clock time: Internal representation of time, given by the phase of endogenous rhythms (e.g., reproductive state; subjective midnight), and can determine an organism's response to an environmental factor.

Masking: An effect by an environmental factor that directly modifies the expression of an overt rhythm; masking may augment (positive masking) or suppress (negative masking) the amplitude of a rhythm or alter its measured phase.

Oscillator: A system capable of producing a regular, periodic fluctuation of an output around a mean.

Period length: Time after which a defined phase of the rhythm re-occurs; i.e., time taken for a full cycle.

Phase: A defined, stable cycle-to-cycle reference point within the cycle of a rhythm (for example, start of activity).

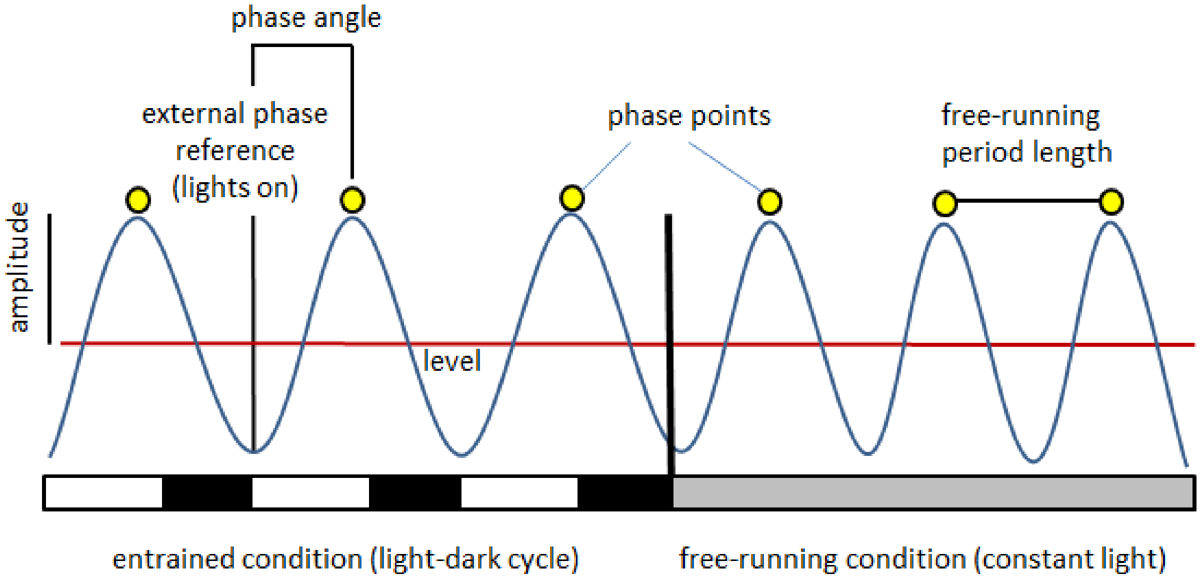
Phase angle of entrainment: The time difference (phase relationship) between a defined phase of a behavioural or physiological rhythm and an external phase-reference (e.g., time of sunrise)

Phenotypic plasticity: The property of a genotype to produce different phenotypes in response to different environmental conditions.

Reaction norm: A function that describes the phenotypic response of a given genotype to variations in factors of the environment.

Zeitgeber (time-giver; "entraining cue"). A periodic external signal capable of entraining a biological rhythm; in circadian context light is the predominant zeitgeber. Zeitgebers do not induce a rhythm but determine its period length and set its phase angle.

Inlay: Terminology of biological rhythm. The graph shows a schematic circadian rhythm (e.g, in body temperature). On the left hand side, it is entrained to the light – dark cycle, on the right hand side it is free-running under constant light. The graph highlights defined phase points (here, peaks; indicated by yellow dots), period length as the time taken for a full cycle between two phase points, and amplitude and level of the rhythm; it also shows phase angle (potentially chronotype) as the difference between an external phase reference (here, lights on) and the phase point.



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