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Preface

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One contribution of 12 to a theme issue 'Wild clocks: integrating chronobiology and ecology to understand timekeeping in free-living animals'.

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Wild clocks: preface and glossary

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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 (e.g. [1–3]). Sixty years ago, a diagram appeared in a book of papers from the Fifteenth Symposium for the Study of Development and Growth (figure 1; [4]) 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. Figure 1 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' [4], 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 programmes of the two fields became non-overlapping, with chronobiologists focusing on unravelling 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' [5].

The time is now ripe to reinvigorate a truly synthetic approach. We now have at hand: tools to record, analyse 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', 15–20 March 2015) seeks to catalyse such a reunification, highlighting new advances and approaches that can address the interdependence of chronobiology and ecology. In the following 11 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

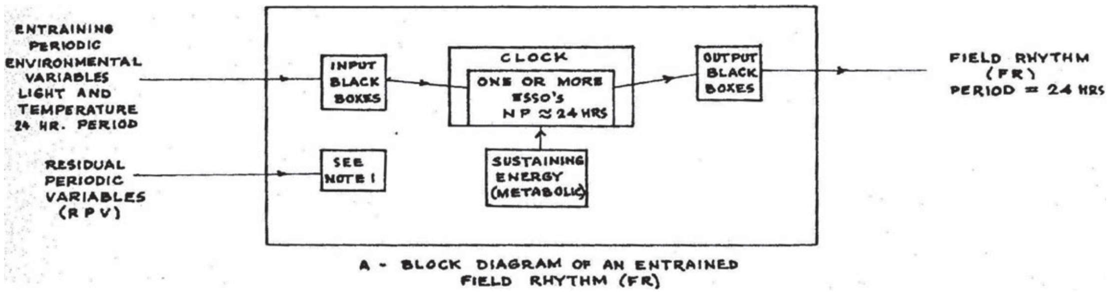

Figure 1. Block diagram of an entrained field rhythm (FR). NP, natural period.

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 [6]. 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 [7]. 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 [8]. 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 [9].

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 [10], in timely activation from diapause and other insect lifecycle stages [11] and in enabling migratory species to exploit geographically distant resource pulses [12]. These reviews are followed by an in-depth look at intra-specific variation in timing from an evolutionary standpoint. 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 [13].

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 [14]. Then, the importance of such interactions is highlighted based on an exemplary system, the finely timed coevolution between flowering plants and their pollinators, which ultimately affects species interactions up to community levels [15]. 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 [16].

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 [17,18]. 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.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

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Editor profiles

William J. Schwartz is a Professor of Neurology, Dell Medical School, and Integrative Biology, College of Natural Sciences, The University of Texas at Austin, where he is also the Associate Chair for Research and Education in the Department of Neurology. For four decades, Schwartz's research has focused on the regulation of mammalian circadian rhythmicity by the master clock in the hypothalamic suprachiasmatic nucleus, using laboratory models. Most recently, his laboratory has been analysing the possible role of social interactions in shaping rhythms in animals living together as couples or in groups, a biotic factor that likely strongly influences Wild Clocks.

Barbara Helm is a Reader at the Institute of Biodiversity, Animal Health and Comparative Medicine of Glasgow University (UK), where she conducts research at the intersection of physiology and ecology. Previously, she had long worked at the Max Planck Institute for Ornithology in Andechs, Germany. Helm's research is inspired by her equal fascination with biological rhythms and wild birds. Owing to their highly mobile lifestyle, birds are expert timekeepers, and nowhere is this more evident than in their daunting periodic migrations. Among the many rhythmic processes that Helm studies, migration, thus, is perhaps the most emblematic of Wild Clocks.

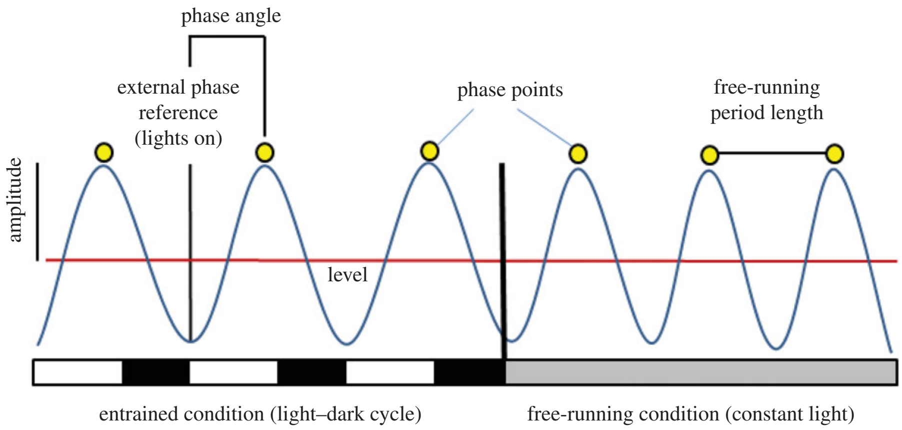
Menno P. Gerkema is a professor at the University of Groningen in the Faculty of Science and Engineering. He holds a chair in Chronobiology and in Science, Business and Policy. He is co-founder of Chrono@Work. The main focus of his chronobiological scientific work is on ultradian rhythms in animal behaviour, on neurophysiological regulation of circadian output, on mechanisms of daily memory and on the evolutionary perspective of night- and day active behaviour. In his career, he preferably worked with animal models he also could observe in field conditions, like wrasses, starlings, dunnarts, house mice and voles.

References

1. Daan S, Aschoff J. 1982 Circadian contributions to survival. In *Vertebrate circadian systems: structure and physiology* (eds J Aschoff, S Daan, GA Groos), pp. 305–321, Berlin, Germany: Springer.
2. Enright JT. 1970 Ecological aspects of endogenous rhythmicity. *Annu. Rev. Ecol. Syst.* **1**, 221–238. (doi:10.1146/annurev.es.01.110170.001253)
3. Dunlap JC, Loros JJ, DeCoursey PJ 2004 *Chronobiology: biological timekeeping*. Sunderland, MA: Sinauer Associates.
4. Pittendrigh CS, Bruce VG. 1957 An oscillator model for biological clocks. In *Rhythmic and synthetic processes in growth* (ed. D Rudnick), pp. 75–109. Princeton, NJ: Princeton University Press
5. Halle S, Stenseth NC (eds). 2000 *Activity patterns in small mammals: an ecological approach. Ecological studies*, vol. 141, Berlin, Germany: Springer-Verlag.
6. Helm B, Visser ME, Schwartz W, Kronfeld-Schor N, Gerkema M, Piersma T, Bloch G. 2017 Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Phil. Trans. R. Soc. B* **372**, 20160246. (doi:10.1098/rstb.2016.0246)
7. Dominoni D, Åkesson S, Klaassen R, Spoelstra K, Bulla M. 2017 Methods in field chronobiology. *Phil. Trans. R. Soc. B* **372**, 20160247. (doi:10.1098/rstb.2016.0247)
8. Rattenborg NC, de la Iglesia HO, Kempenaers B, Lesku JA, Meerlo P, Scriba MF. 2017 Sleep research goes wild: new methods and approaches to investigate the ecology, evolution and functions of sleep. *Phil. Trans. R. Soc. B* **372**, 20160251. (doi:10.1098/rstb.2016.0251)
9. van der Veen DR, Riede SJ, Heideman PD, Hau M, van der Vinne V, Hut RA. 2017 Flexible clock systems: adjusting the temporal programme. *Phil. Trans. R. Soc. B* **372**, 20160254. (doi:10.1098/rstb.2016.0254)
10. Williams CT, Klaassen M, Barnes BM, Buck CL, Arnold W, Giroud S, Vetter SG, Ruf T. 2017 Seasonal reproductive tactics: annual timing and the capital-to-income breeder continuum. *Phil. Trans. R. Soc. B* **372**, 20160250. (doi:10.1098/rstb.2016.0250)
11. Denlinger DL, Hahn DA, Merlin C, Holzapfel CM, Bradshaw WE. 2017 Keeping time without a spine: what can the insect clock teach us about seasonal adaptation? *Phil. Trans. R. Soc. B* **372**, 20160257. (doi:10.1098/rstb.2016.0257)
12. Åkesson S, Ilieva M, Karagicheva J, Rakhimberdiev E, Tomotani B, Helm B. 2017 Timing avian long-distance migration: from internal clock mechanisms to global flights. *Phil. Trans. R. Soc. B* **372**, 20160252. (doi:10.1098/rstb.2016.0252)
13. Hau M, Dominoni D, Casagrande S, Buck CL, Wagner G, Hazlerigg D, Greives T, Hut RA. 2017 Timing as a sexually selected trait: the right mate at the right moment. *Phil. Trans. R. Soc. B* **372**, 20160249. (doi:10.1098/rstb.2016.0249)
14. Kronfeld-Schor N, Visser ME, Salis L, van Gils JA. 2017 Chronobiology of interspecific interactions in a changing world. *Phil. Trans. R. Soc. B* **372**, 20160248. (doi:10.1098/rstb.2016.0248)
15. Bloch G, Bar-Shai N, Cytter Y, Green R. 2017 Time is honey: circadian clocks of bees and flowers and how their interactions may influence ecological communities. *Phil. Trans. R. Soc. B* **372**, 20160256. (doi:10.1098/rstb.2016.0256)
16. Bulla M, Oudman T, Bijleveld AI, Piersma T, Kyriacou CP. 2017 Marine biorhythms: bridging chronobiology and ecology. *Phil. Trans. R. Soc. B* **372**, 20160253. (doi:10.1098/rstb.2016.0253)
17. Hölker F, Wolter C, Perkin EK, Tockner K 2010 Light pollution as a biodiversity threat. *Trends Ecol. Evol.* **25**, 681–682. (doi:10.1016/j.tree.2010.09.007)
18. Stevenson TJ *et al.* 2015 Disrupted seasonal biology impacts health, food security and ecosystems. *Proc. R. Soc. B* **282**, 20151453. (doi:10.1098/rspb.2015.1453)
19. Daan S, Merrow M, Roenneberg T. 2002 External time - Internal time. *J. Biol. Rhythms* **17**, 107–109. (doi:10.1177/074873002129002375)
20. Roenneberg T. 2015 Having trouble typing? What on earth is chronotype? *J. Biol. Rhythms* **30**, 487–491. (doi:10.1177/0748730415603835)

Glossary: definitions of key terms

Abiotic time	All aspects of geophysical cycles and their climatic correlates, 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, parasites, predators and prey.
Chronotype	Characterization 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 (e.g. early versus 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 [19].
Free-running rhythm	The endogenous rhythm exhibited under constant conditions, characterized 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 [19,20].
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 (e.g. start of activity).
Phase angle of entrainment	The time difference (phase relationship) between a defined phase of a behavioural or physiological rhythm (e.g. start of activity) 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.



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 circles), 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.