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# Chapter 26

## Circannual Rhythms Anticipate the Earth's Annual Periodicity

Barbara Helm and Gerald A. Lincoln

**Abstract** Life on Earth has evolved in a periodic world, which in most environments cycles predictably between conditions that are favourable or unfavourable for an organism. Organisms use favourable seasons to reproduce and grow, and withdraw during unfavourable seasons. To deal with the predictable changes in their environments, all taxonomic groups have evolved genetically programmed timing mechanisms. These govern seasonal cycles in physiology and behaviour that optimise survival and reproductive success, and have been formally described as circannual rhythms. Experimentally, under conditions of constant day length and temperature, circannual rhythms of many species continue to be expressed, even throughout the life cycle, illustrating the fundamental endogenous control. Under natural conditions, they are usually entrained by seasonal time cues, notably photoperiod, to synchronise the biology to environmental periodicity. Here we review long-term timekeeping strategies from classical vertebrate models to invertebrate and unicell life histories. These circannual rhythms enable organisms to anticipate Earth's periodicity.

### 26.1 Evolution in a Periodic World

On an annual timescale, environmental conditions in which living organisms have evolved are just as fundamentally periodic as described in the preceding sections for daily rhythmicity [1]. All but the equatorial regions undergo annual cycles of exposure to the sun because of the tilt of Earth's axis ( $23.5^\circ$ ) relative to its orbit around the sun (Fig. 26.1). The daylight fraction of the 24 h day (i.e., photoperiod) is longer in summer than in winter, and the amplitude of the annual photoperiodic cycle increases with increasing latitude. The annual change in exposure to solar radiation has a whole suite of effects on organisms' environment, beyond

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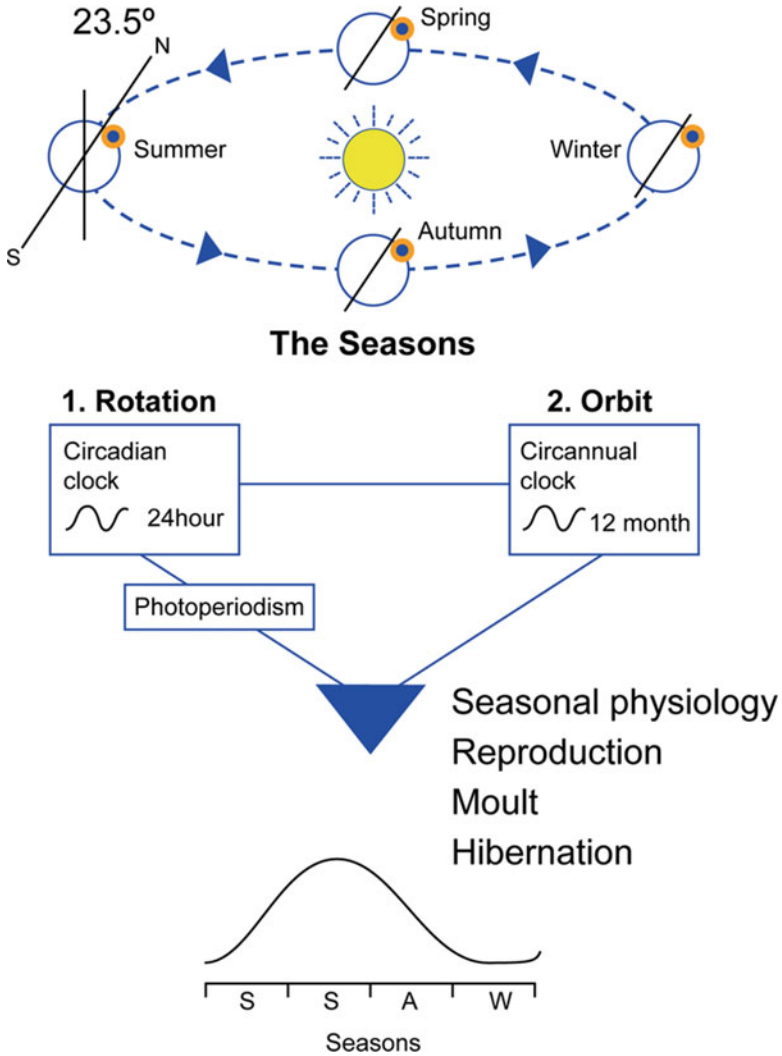
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**Fig. 26.1** Endogenous clocks anticipate the Earth’s periodicities. The rotation of the Earth on its axis every 24 h (*line S/N* indicates the rotational axis and the *filled circle* represents a point of reference) and orbit around the Sun every 12 months has favoured the evolution of endogenous circadian and circannual clocks. The ability to respond to the annual cycle in day length (photo-periodism) depends on the circadian clock system. Organisms utilise both types of innate timing mechanism to regulate long-term cycles in reproduction, moul, hibernation and other seasonal characteristics (Adapted from [63])

differences in day length. For example, solar exposure affects ocean and land temperatures and, as a consequence, humidity, cloud cover, precipitation, snow cover and air and ocean currents. These knock-on effects lead to annual fluctuations in climatic conditions on a global scale, even at regions that are not directly exposed

to changing photoperiod (such as equatorial or deep sea locations). However, both the amplitude of seasonal changes and the precision in timing differ between locations on Earth.

Living conditions of organisms across the globe are shaped by annual cycles in climate. For example, while organisms at higher latitudes have to cope with alternation between summer and winter seasons, changes between dry and rainy seasons can be similarly challenging for organisms living near the equator. Both plants and animals respond to these annual changes by aligning their biology, using favourable conditions for reproduction and growth, while investing into survival of unfavourable conditions. Consequently, in most parts of the globe, vegetation cover spreads and retracts rhythmically, followed by pulses of animal abundance. This phenomenon has been described as a 'green wave' for habitats as diverse as Serengeti and the Russian Arctic [2, 3]. By undergoing pervasive seasonal changes, the biotic environment effectively potentiates geophysical cycles. Its rhythmicity fundamentally affects the quantity and quality of available food, as well as risks such as predation and infection. These factors have been termed 'ultimate' causes of seasonal life histories because they exert selection pressure on individuals and thereby drive evolution [4, 5].

The most obvious rhythmic response of organisms is alternations between active or reproductive stages and dormant, or reproductively inactive, stages. Examples of inactivity include the annual dieback of deciduous perennial plants to their rootstock, encystment of protists and bacteria to permanent stages, diapause of insects and hibernation of vertebrates. The annual life cycle of organisms often includes further periodic changes in morphology, physiology and behaviour, including moult and migration (cf. Chap. 30). Alternations may occur within individuals, at different stages of the life history (e.g. eggs, larvae, pupae) and transgenerationally (e.g. multiple generations in insects within a year). The particular strategies vary markedly depending on habitat and species' characteristics [6]. For example, in noctuid macro-moths on the British Isles, the most common strategy for survival through winter is the larval stage (48 % of species), and the least common is imago (7 %; G. Lincoln, pers. observation).

It is crucial for the fitness of organisms that these changes are accurately timed. Transitions between stages often require many weeks or months, for example, the growth of the vegetative body of plants, the recrudescence of the reproductive system in mammals and the return of migratory birds from their winter quarters. In order to reproduce at the optimal time, organisms must be able to anticipate future environmental conditions and initiate preparations far in advance. In mammals, the requirement for a long gestational period means that ovulation must be timed to occur many months in advance of the birth season, when environmental conditions will favour survival of the offspring [1]. This example illustrates that timing often cannot be cued by the ultimate causes and instead responds to 'proximate' causes [4]. Photoperiod is the most reliable, proximate predictor of future conditions and is used by most organisms to anticipate the seasons [7, 8]. Other cues include ambient

temperature and changes in food supply and rainfall [1], but organisms must safeguard against following misleading information. For example, in December of 2015, ambient temperatures in northern polar regions were far above freezing. However, initiating summer-type activities under these conditions would be disastrous for polar species.

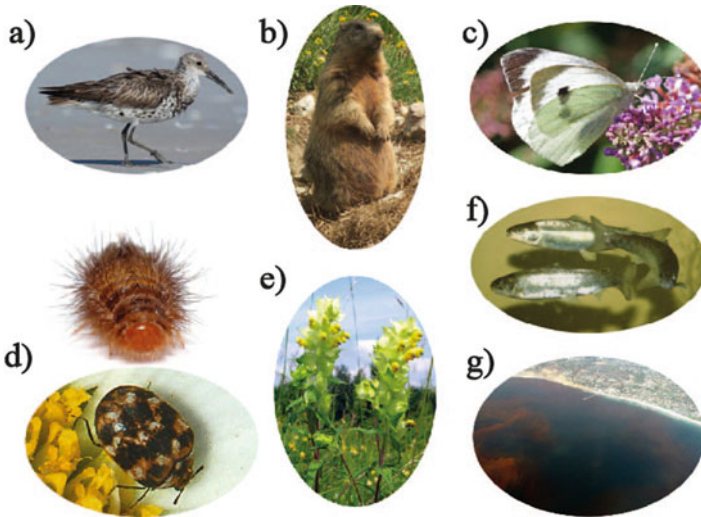
Accordingly, organisms have evolved an internal representation of time, which governs transitions in the life cycle, and proficient use of environmental cues to time these transitions. Such an internalisation of time has been a key, ancient innovation for coping with seasonal environments [7]. Therefore, across taxa in biology, organisms show genetically programmed, endogenous timing mechanisms. These are modified according to the particular, local environments of individuals and populations. The annual processes can occur periodically under constant environmental conditions and are formally described as circannual rhythms (Latin derivation: *circa* = about and *annus* = year).

## 26.2 Discovery of Circannual Rhythms

Naturalists and researchers have long speculated that organisms must be utilising internal timekeeping mechanisms on an annual timescale. This was based on observations in the wild, rather than on experimental evidence, because long-term studies in isolation from direct influences of the environment were not feasible. In the twentieth century, when experimental capacities were expanded, the evidence for truly endogenous rhythms was consolidated for species across many taxa [9]. Here we illustrate a small selection of examples (Fig. 26.2 [10]).

Few species have captured human interest more than migratory birds (Fig. 26.2a; great knot, *Calidris tenuirostris*). Throughout recorded history, farmers and naturalists have noted their timely return, which is so accurate that in some societies their behaviour is used as an agricultural calendar [1]. Birds were also observed in captivity, and from the eighteenth century, ornithologists described behavioural changes during the migration seasons. Captive songbirds of nocturnally migrating species showed migratory restlessness (*zugunruhe*), hopping and flying at night in their cages, while their wild conspecifics would engage in actual migration [11–13]. This initial evidence for innate migration clocks was then supported by new evidence on the migration patterns of birds. A striking example is the common cuckoo (*Cuculus canorus*) which winters in Africa. The offspring are raised by foster parents and migrate independently to their species' wintering grounds, illustrating an innate sense of time ([9, 14, 15]).

Another group of animals that had long invited speculation about timekeeping are hibernating mammals [15]. Hibernation often occurs in underground burrows, which may be sealed by the animals with plugs and become covered by thick layers of snow (Fig. 26.2b; alpine marmot, *Marmota marmota*). It is hard to conceive how their timely arousal in spring is achieved, other than by the control of some form of an endogenous clock. Indeed, studies of hibernating ground squirrels (*Citellus*



**Fig. 26.2** Model organisms for circannual rhythm research. Many different species have been used experimentally to demonstrate the endogenous nature of long-term cycles. The classic paradigm is to house the test subject in the laboratory under constant conditions of temperature, day length and food supply for more than a year and to repeatedly monitor morphological, physiological and behavioural characteristics. In the species illustrated, the cyclical biology persisted in the absence of environmental cues, thus suggesting innate control. Because the period of the free-running cycles differs from a year, the rhythm is termed circannual. Under natural conditions, outdoors, periodic seasonal environmental cues act to extend or condense the innate cycle to 12 months and to synchronise its phase to the optimal time of year. Time control affects a wide range of characteristics (e.g. body weight, food intake, gonadal activity, moult, migration and hibernation) and is specific for each species. (a) Migrating bird, great knot (*Calidris tenuirostris*; by sunphlo); (b) hibernating mammal, alpine marmot (*Marmota marmota*; by trldp); (c) emerging butterfly, large white butterfly (*Pieris brassicae*; by Gerald Lincoln); (d) pupating beetle, varied carpet beetle (*Anthrenus verbasci*; larval form, frontal view by André Karwath, adult form by Hectonichus); (e) germinating plant, yellow rattle (*Rhinanthus alectorolophus*; by Bernd Haynold); (f) smoltifying Atlantic salmon (*Salmo salar*; by E. Peter Steenstra/USFWS); (g) blooming algae ('red tide', mainly *Alexandrium tamarense*; nn). Images except for (c) licenced under public domain via [wikimedia.org](https://www.wikimedia.org); design: Edda Starck

*lateralis*) provided the first, unequivocal evidence that isolated, individually marked animals show persistent circannual rhythms under constant environmental conditions of light and temperature [16]. These circannual rhythms are not exclusive to the animal kingdom, but also occur in primitive plant species, including marine kelp (brown algae, Phaeophyceae [17]).

While circannual rhythms occur within individuals, some can only be characterised at a population level. These include the timing of transitions between modular stages of development in insects, for example, from egg to larval to pupal to adult. Here, the timing programme gates windows of opportunity for developmental transitions that periodically open and close, but each individual undergoes a given transition only once in its life time. For example, many species of butterfly

show staggered emergence of adults [18]. Of each cohort of pupae, only some produce adults in a given year, while the others wait in pupal stage for another 1 or several years before emerging. One such species is the large white butterfly (Fig. 26.2c; *Pieris brassicae*; Jeanne Robinson, pers. comm.). Circannual rhythms in the frequency of developmental transitions have been characterised in great detail for the varied carpet beetle, *Anthrenus verbasci* (Fig. 26.2d [19]). Pupation of carpet beetles occurs mostly in the first year of larval development, but part of the cohort will suspend this phase and pupate 1 or 2 years later. The population-level circannual rhythm of carpet beetles shares many features with that of circadian rhythms [20]. Another fascinating but still poorly understood example of insect developmental rhythms with extremely long period length is that of periodical cicadas (Hemiptera), whose life cycle lasts up to 17 years. Adults emerge highly synchronously from nymphs, but the periodicities and years of emergence differ between species and regions, indicating innate control [21]. Similar population rhythmicity has also been documented for seasonal events in plants, for example, seed germination of yellow rattle (Fig. 26.2e; *Rhinanthus alectorolophus* [22]), and in vertebrates, for example, the smoltification and migration of salmonid fish (Fig. 26.2f; *Salmo salar* [7]).

Years after the characterisation of endogenous circannual rhythms in multicellular organisms, researchers were surprised to find such rhythms even in unicellular protists [23]. The marine dinoflagellate *Alexandrium tamarense*, which is a major contributor to algal bloom (Fig. 26.2g, ‘red tide’), shows circannual rhythmicity in the propensity of a population of cysts to germinate. Because of its tractability and the simplicity of unicellular organisation, this species has recently attracted major interest of researchers who hope to decode the mechanistic basis of circannual rhythmicity (cf. Chap. 29).

### 26.3 The Paradigm of Inherent Rhythms Under Constant Conditions

As detailed above for circadian rhythms, an important stage in the understanding of a biological rhythm requires the documentation of its truly endogenous, self-sustained nature in isolated test subjects in the absence of any environmental time cues. To be considered rigorous evidence for endogenous regulation, biological rhythms must free-run with an individual period length (called ‘ $\tau$ ’), indicated by drift from environmental time [24]. Observed rhythms with a period length that matches those of geophysical cycles cannot be distinguished from direct responses to uncontrolled environmental factors, but may have an equally endogenous basis. To identify period length, two or more sequential cycles must be documented, which for circannual rhythms was a pain-staking process because of the long timescale. However, from the late 1950s onward, such evidence was provided in quick succession for insects, mammals and birds and then subsequently for various

other organisms (Fig. 26.2 [9]). Many circannual studies recorded a whole suite of behavioural and physiological processes within individual subjects, for example, changes in reproductive organs, moult, annual activity patterns and body mass. These processes were shown to recur with period lengths that deviated significantly from the solar year, most typically being short at around 10 months, although in some taxa free-running cycles were consistently longer than 365 days (e.g. great knot; Fig. 26.2a [25]). A remarkable finding of some of these studies was that in many cases, different annual processes desynchronised within the body, for example, moult relative to reproductive cycles [9, 25, 26]. These observations show that circannual rhythms entail independent, presumably tissue-specific processes and do not arise as a mere by-product of sequences of physiological stages [10].

Figure 26.3 shows two examples of extraordinarily long circannual studies. The persistence of the free-running rhythm was recorded for more than 10 years in a tropical songbird, the stonechat (*Saxicola torquata* [5, 27]), and in a hibernating ground squirrel, the chipmunk (*Tamias sibiricus* [28]). In stonechats in particular, the truly innate nature of circannual rhythms has been highlighted by the observations that the rhythms developed spontaneously even in birds that were bred and born under constant conditions and lasted for the entire life cycle (Fig. 26.3a [12]).

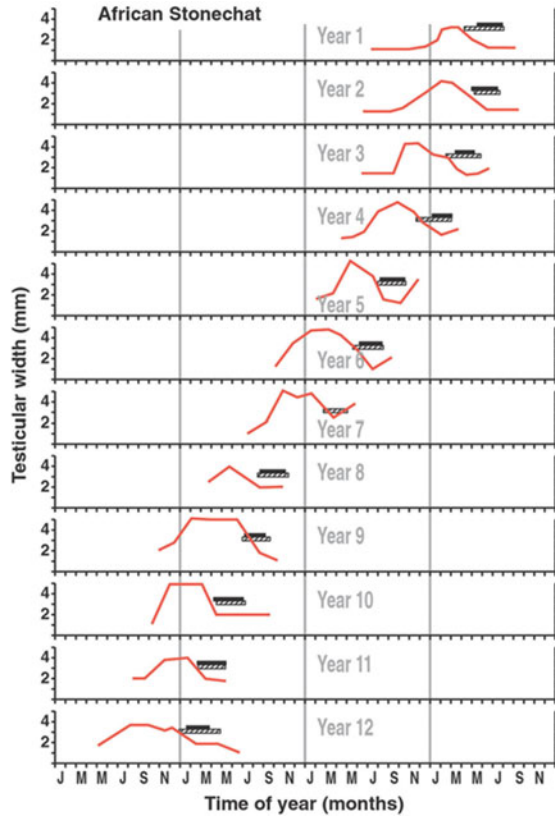
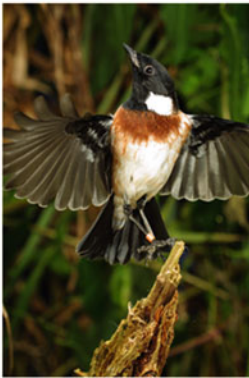
In such rigorous studies, subjects were held under conditions of constant food supply, temperature and light. The definition of constant light conditions for circannual studies has been controversial. The most commonly used constant condition was a daily light-dark (LD) cycle of 12L:12D h. This condition occurs at any location on Earth at least twice a year (during the equinoxes) and has been seen as a relatively neutral test condition, much like twilight in circadian rhythm research. However, the 12L:12D h light cycle conveys a specific seasonal signal. Critics have therefore argued that circannual rhythms were physiological artefacts in response to this specific light condition. This criticism was met by documentation from key examples in insects, birds and mammals of free-running cycles in the absence of LD cycles, for example, under continuous dim light, bright light or darkness [20, 28, 29].

While such evidence shows that the expression of circannual rhythms is generally not dependent on a particular light condition, species differ widely in the requirements under which circannual rhythms are expressed. For example, in some species, photoperiodic cues during particular phases of the rhythm are required to advance the rhythm, and in some others, the permissive range entails only a narrow band of constant day lengths (e.g. from above 11.5 to below 12.5 h in the European starling, *Sturnus vulgaris* [30]). Such differences between organisms are intriguing and can give leads to the functional context and mechanistic organisation of circannual rhythms. However, caution needs to be applied when interpreting the presence and absence of circannual patterns under constant conditions. The main function of the constant-condition paradigm is documentation of endogeneity and formal properties of circannual rhythms. This experimental paradigm is highly artificial and contrasts with the real-life environment for which circannual rhythms have evolved. Therefore, hereafter, this chapter will go beyond



# a) Stonechat

Circannual rhythms throughout the life cycle  
(LD 12:12)  $\tau = 10.5 \text{ mo}$



**Fig. 26.3** Circannual rhythms that are sustained across the life history. Two examples where circannual rhythmicity has been shown to persist throughout life in animals maintained under constant conditions. *Above:* African stonechat. Cycles in testis diameter and feather moult in a tame, individual bird caged in the laboratory under constant photoperiod (12L:12D h) throughout its 12-year life span. Reproductive and moult cycles persisted with a free-running period ( $\tau$ ) of 10.5 months: the periodic peaks in gonadal activity became progressively earlier in real time, phase-advancing by a complete cycle. The moult cycle followed a similar pattern and coincided with gonadal regression (Adapted from [64]; image Gerhard Hoffmann). *Below:* chipmunk. (a) Circannual body temperature cycles in individual chipmunks housed indoors under constant cool temperature (5 °C) and *dim* light for up to 11 years. The *filled bars* represent the periods of hyperthermia associated with hibernation: *HC* hibernation cycle (time from onset to next onset of hibernation, *HD* hibernation duration: values mean  $\pm$  SEM). (b) Mean period length for the temperature/hibernation rhythm for 16 individual chipmunks under constant conditions (mode, 10.5 months). (c) Circannual cycles in the blood concentration of specific liver proteins (called hibernating proteins, HP) in one representative chipmunk related to the temperature/hibernation rhythm (periodic *filled bars*) and western blots of the concentrations of the three different HP proteins that form a complex in the blood. The HP 27 protein is shown to dissociate at the choroid plexus of the brain entering the CSF and affects the cold resistance of brain tissue as part of a seasonal adaptation (Adapted from [28]; image: AndiW, [wikimedia.org](http://wikimedia.org))

## b) Chipmunk

Hibernating proteins made by the liver

$\tau =$   
10.5 months

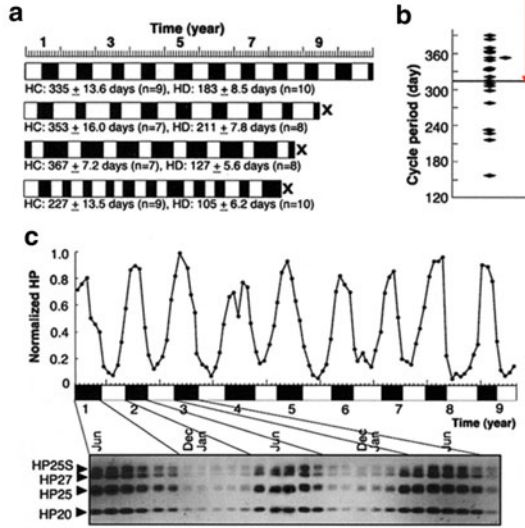


Fig. 26.3 (continued)

discussing examples that have been formally tested under rigorous constant conditions.

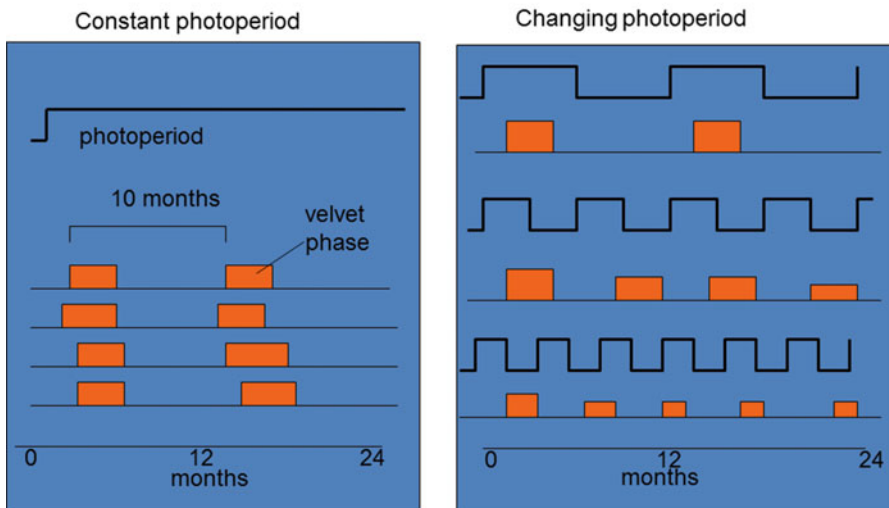
## 26.4 Synchronisation to the Environment

Although circannual rhythms free-run under constant conditions, under natural conditions outdoors, they are usually entrained to the Earth's periodicity by annual time cues (*zeitgebers*). In the vast majority of investigated species, even in the tropics, the periodicity of life cycle stages matches the solar year. Just like circadian rhythms, circannual rhythms have evolved to closely interact with *zeitgebers*, particularly day length, to adjust the phase and speed (angular velocity [9]) of the cycle (Chap. 29). The only non-photic factor that has been shown to have some *zeitgeber* effects is ambient temperature [14].

Many species respond very strongly to changes in day length [7, 8]. Photoperiodism occurs throughout global environments, but responses are generally strong at temperate and high latitudes where the timing of seasonal transitions is predictable, and photoperiod is a reliable *zeitgeber*. The entraining effect of photoperiod can be very dominant driving multiple cycles within 1 year under artificial conditions, e.g. antler cycles in sika deer (*Cervus nippon* [31] Fig. 26.4a). The role of the innate

circannual time mechanisms cannot be revealed in outdoor conditions because it is entrained by the dominant influence of photoperiod, but it still operates. This has been elegantly demonstrated in sheep, where the effect of photoperiod has been silenced by removal of the pineal gland, whose production of the hormone melatonin propagates the photoperiodic signal (Fig. 26.5a). Removal of the pineal signal reveals the endogenous control of the breeding cycle, which free-runs under natural light conditions until the effect of photoperiod is reinstated using periodic programmed infusions of melatonin [32]. The studies convincingly demonstrate

## a) Antler cycles in Sika deer



**Fig. 26.4** Circannual cycle timed by changes in day length (photoperiod). (a) Antler cycles in sika deer, *Cervus nippon*. *Left panel*, periodic antler cycles (orange bar represents the antler growth phase; velvet) in four individual deer housed in a barn under constant long photoperiod (16L:8D h). The antlers are replaced every 10 months due to the endogenous circannual regulation of the seasonal reproductive cycle. *Right panel*, periodic antler cycles in individual sika deer housed under artificial changes in photoperiod (abrupt switches between long days 16L:8D and short days (8L:16D – see horizontal line): *top*, once every 12 months; *middle*, twice every 12 months; *bottom*, three-times every 12 months. The accelerated light transitions induced up to three antler cycles within the normal year (driving the circannual cycle in an extreme manner). The treatments altered the phase angle between the light change and timing of the reproductive cycle consistent with an entraining effect on the endogenous circannual timer system (Adapted from [31]). (b) Antler cycles (orange bar) and sexual cycles (black bar; rut) under natural lighting conditions at London Zoo (54° N). *Top*, sika deer show a synchronised autumn rutting season; *middle*, Pere David's deer, *Cervus davidii*, show a synchronised summer rutting season (due to a phase-shifted circannual timer); *bottom*, axis deer (*Axis axis*; data for ten individuals) show annual, asynchronous rutting seasons. This tropical species is non-photoperiodic: having been kept at the zoo at a temperate latitude for over 100 years, the stags still show a seasonality (Adapted from [17, 38]; image: young stags with hard and velvet antlers, respectively; by sumeet.moghe at Wikipedia)

## b) Circannual rhythms in deer

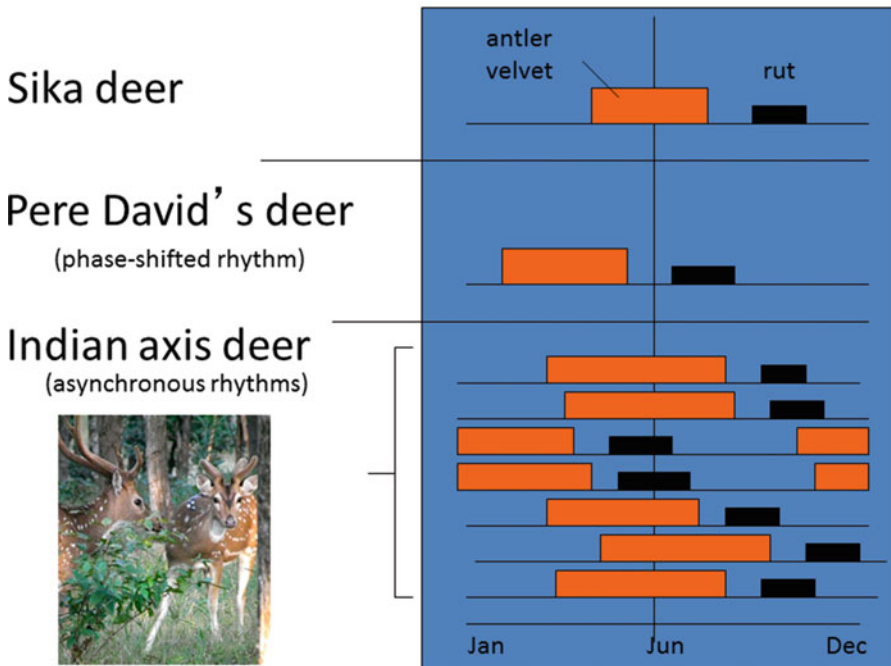


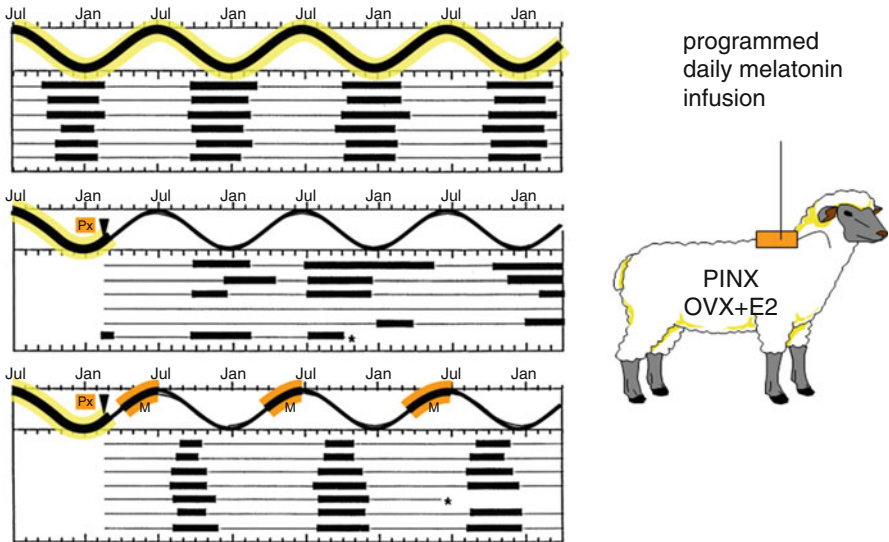
Fig. 26.4 (continued)

that in sheep, it is the long photoperiod signal of summer that acts to entrain the endogenous circannual system, setting the onset of breeding to the autumn.

Formally, entrainment to zeitgebers has been described in many species and is very similar to that of circadian rhythms. In species with robust circannual rhythms, such as woodchuck (*Marmota monax*), entrainment involves transients (i.e. several intermediate cycles before assuming the final phase of entrainment; P. Concannon cited in [10]). Conversely, species with more responsive circannual rhythms, such as carpet beetles (Fig. 26.2d), show entrainment via fast resetting (type 0 response [20]). These patterns are formally described as circannual phase response curves and have been published for several species [22, 33].

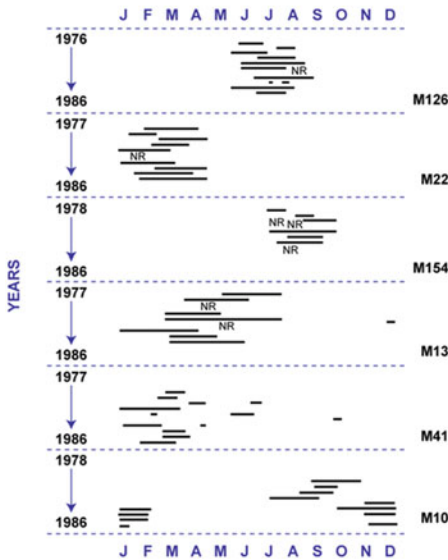
In addition to differences in entrainment properties, species and even local populations may differ in the phase they assume relative to a given photoperiodic cycle (e.g. stonechats, Fig. 26.3a; Helm et al. [34]). In species from different environments, specific seasonal behaviours may occur at various times of year and under a broad range of photoperiods. For example, in temperate regions a given bird species may breed under increasing spring day lengths, but in arid environments, the same species may breed under short days in winter [10]. Similarly, in mammals, the closely related species of sika and Pere David's deer (*Cervus davidii*; Fig. 26.4b) differ considerably in the timing of the rut. When such species are housed under similar conditions (i.e. under 'common garden' conditions), the

## Photoperiod entrains the circannual reproductive rhythm



**Fig. 26.5** Entrained circannual rhythms. (a) Photoperiodic entrainment of circannual rhythms in sheep. This elegant study investigated the effect of pinealectomy and melatonin replacement on the expression of circannual rhythms in gonadotropin secretion in female Suffolk sheep (*black horizontal bars* represent the sexually active phase for each individual animal). *Top panel*, control group ( $n=6$ ), untreated, intact animals living outdoors under the natural cycle of day length (represented by the sign wave); note the occurrence of synchronous annual cycles with the sexually active phase in autumn. *Middle panel*, pinealectomized group ( $n=6$ ), pineal gland removed in spring (Px); note the occurrence of more erratic, asynchronous seasonal reproductive cycles due to the removal of the photoperiod-melatonin relay mechanism. *Bottom panel*, melatonin replacement group ( $n=7$ ), Px in spring and then treated periodically for 3 months each summer (*orange block*, M) with programmed daily infusions of melatonin (8 h/day to mimic a long day); note the re-synchrony and normal phasing of the seasonal reproductive cycles. Animals treated with programmed infusions of melatonin 16 h/day to mimic a short day failed to show this response (data not shown). Conclusion: long days of summer act to entrain the endogenous circannual clock that regulates seasonal reproduction – this sets the phase of the breeding season to the autumn. All animals were ovariectomised and given an estradiol implant (OVX + E2) to provide a stable sex steroid state (Adapted from [32]). (b) Asynchronous annual cycles of free-living male African elephants in Amboseli National Park (Kenya). Fully mature bulls undergo annual cycles of musth (i.e. phases of elevated testosterone with associated physiological and behavioural changes). Each male adopts his preferred annual mating time that is consistent over successive years, but the time varies markedly between males. These specific chronotypes reduce male-male confrontation and allow males to maximise mating opportunities. While it is clear that these animals are closely keeping track of time, the phase of their annual cycles is not driven by photoperiod (Adapted from [39]; image: African elephant bulls in mock fighting; by Profberger at English Wikipedia)

## Musth Cycles of African Elephants



Asynchronous annual  
musth cycles in six  
Amboseli elephant bulls

Fig. 26.5 (continued)

differences in breeding patterns persist, indicating an innate basis. Furthermore, breeding programmes that looked at inheritance in hybrids showed unambiguously that these differences can be based on genetic control (e.g. stonechats, Fig. 26.3a [5]). The genetic differences in the timing may be based on evolutionary modification of the circannual rhythm generation mechanism (e.g. control of period length or of the photoperiodic response mechanism [7, 34]).

Despite the proven strength of photoperiod as a zeitgeber, some species, or individuals within species, are non-photoperiodic. They may be arrhythmic (e.g. American white-footed mice, *Peromyscus leucopus*), or show free-running circannual patterns, or show annual, but asynchronous, cyclicality [35]. Circannual cycles in the wild that clearly deviate from the solar year have been reported for species that inhabit relatively constant habitats, in particular, for seabirds from tropical and subtropical regions [5]. A well-known example are sooty terns (*Onychoprion fuscatus*), whose individual breeding cycles on Ascension Island show average periodicities of approximately 10 months [36].

Annual, but asynchronous, cyclicality has been reported from captivity and the wild. Indian axis deer (*Axis axis*; Fig. 26.4b) translocated to the London Zoo retained individual annual cycles which remained out of phase with each other under the strongly seasonal conditions of Britain. Their asynchronous cycles were confirmed also in captive conditions near the equator [37, 38]. Similarly, free-living male African elephants in Amboseli National Park (Kenya) undergo annual cycles of musth (i.e. phases of elevated testosterone with associated physiological and

behavioural changes) (Fig. 26.5b [39]). Each adult adopts its preferred annual mating time that is consistent over successive years, but the time varies markedly between individuals. While it is clear that these animals are closely keeping track of time, the phase of their annual cycles is not driven by photoperiod.

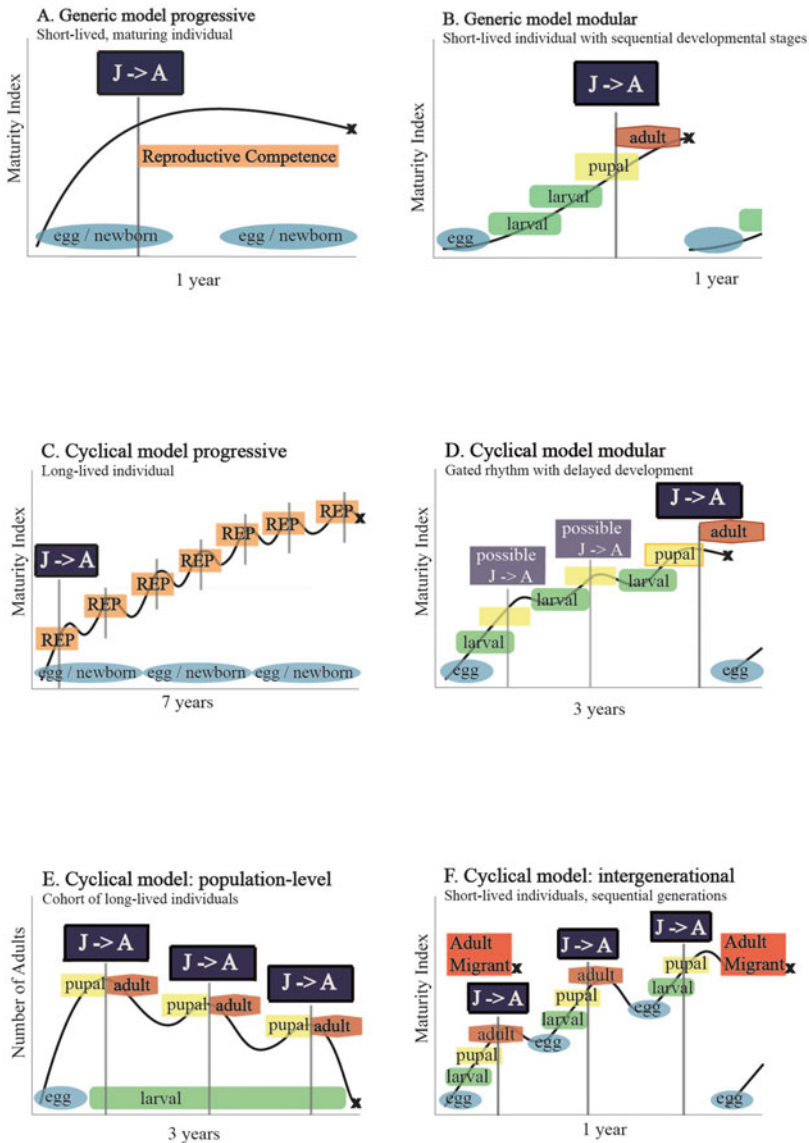
The ability of species to maintain precise timing near the equator, where photoperiod is relatively constant throughout the year, and the lack of responsiveness of some species to photoperiod, has encouraged the search for alternative zeitgebers. Experimental studies have suggested that tropical birds are able to entrain to subtle, non-photoperiod photic cues, for example, to changes in light intensity between dry and rainy seasons and to small changes in the timing of sunrise and sunset [5]. Based on observations from wild species, effects of rainfall, food quality and social factors are also strong candidates as zeitgebers [35]. Overall, these examples provide very good evidence for endogenous circannual time control that is responsive to a range of subtle environmental cues.

## 26.5 Temporal Organisation Within the Life Histories

With very few exceptions, all organisms have to deal with at least some degree of annual periodicity in their environments. Given the great biodiversity on Earth, there is also a great diversity of mechanisms and strategies by which organisms organise their life histories to align with the change of seasons. Above, we have already referred to some of them, and here we develop a classification of annual cycle organisation, exemplified for the transition from juvenile to reproductively active adult (Fig. 26.6). We first show a generic model of the life cycle of an individual for species that live for less than a year (annual species). We distinguish organisms that progressively mature (Fig. 26.6a; e.g. small rodents) from those that have modular development and undergo a series of transitions between distinct stages (Fig. 26.6b; e.g. annual insects [6, 40]). Continuity of the species' life cycle in the first case depends on staggered, overlapping generations (Fig. 26.6a). In the second case, continuity is achieved by a sequence of resistant developmental stages, which can endure challenging conditions, and short-lived, reproductive adults (temporal compartmentalisation; Fig. 26.6b). While timing programmes are involved in these cases, no apparent circannual rhythm exists within individuals.

Individual rhythmicity can emerge from these generic models in longer-lived species (perennial species) in different ways. Individuals of species whose adult form survives for several years usually undergo repeated annual cycles of reproduction and non-reproduction after first reaching maturity (Fig. 26.6c; e.g. larger mammals, birds, kelp). Various modifications of this pattern have been described, adding to the flexibility of annual life cycle organisation. For example, species such as edible dormice (*Glis glis*), which breed best during irregularly occurring overabundance of food, may pause reproduction for several years. This hibernating species samples its environment annually when first arousing and often prematurely returns to hibernation in poor years [41]. Another modification is heterochrony,

## Circannual rhythms as part of the life history programme



**Fig. 26.6** Circannual rhythms within life histories. We present a schematic classification of annual cycle organisation, exemplified for the transition from juvenile to reproductively active adult ( $J \rightarrow R$ ) embedded in the life cycle from egg or newborn to death (indicated by x). We first show generic models of the life cycle of individuals of short-lived species that (a) progressively mature and (b) undergo a series of modular transitions between distinct stages (temporal compartmentalisation). We then show how circannual rhythmicity occurs for these cases in



where the rate of sexual maturation differs relative to other species or even to conspecifics. In avian and mammalian species that delay maturation, a latent circannual rhythm is likely to be present in individuals that gates the timing of possible developmental transitions to adult maturity [42].

In species whose adult life span is short, individual rhythmicity can emerge during earlier, more long-lived developmental stages (Fig. 26.6d; e.g. carpet beetle, Fig. 26.2d). Although individuals transition to reproductive maturity only a single time, during their immature stages, they may have undergone several cycles of a gating circannual rhythm, as described above for heterochrony. On a population level, this can be observed as annual waves of staggered maturation of a study cohort (Fig. 26.6e). This model is highly flexible, allowing, for example, for a species to endure unfavourable seasons in the most resistant stage, such as the cysts of the dinoflagellate *Alexandrium* (Fig. 26.2g; cf. Chap. 29). In all these cases, individuals possess the genetic programme for sustained circannual rhythmicity.

Finally, we draw attention to a variant in which the completion of the annual life cycle involves several sequential generations (Fig. 26.6f). This situation is found in many invertebrates, for example, in the annual migration cycle of the American monarch butterfly (*Danaus plexippus*). In this species, late-summer adults migrate from the northern USA southward to winter quarters in Mexico. In spring, they fly north for part of the way before laying eggs and dying off. Adults produced from these eggs continue this northward journey, followed by one or more further generations that show this phenotype. In late summer, a final generation emerges that has a larger, more robust phenotype and undertakes the long southern migration back to the winter quarters, thus completing the intergenerational life cycle [43]. The mechanisms underlying the regulation of the timing of this multiple-generation life cycle are only beginning to be understood, but each individual and each generation certainly possesses the entire genomic repertoire that is needed for recurrent, circannual rhythms.



**Fig. 26.6** (continued) longer-lived species. (c) If adult forms survive for several years, these adults usually undergo repeated annual cycles of reproduction (“REP”) and non-reproduction after first reaching maturity, although cycles can be omitted and the transition to adult maturity can be delayed (heterochrony). (d) If adult life span is short, individual rhythmicity can emerge during earlier, more long-lived developmental stages. On a population level, this can be observed as annual waves of staggered maturation of individuals from a study cohort (e). Each individual transitions to maturity only once, but in the years leading up to this event, a latent circannual rhythm has likely gated time windows for such transitions. In this way, species can survive in immature endurance stages until a time point is reached for seasonally correct, ephemeral adulthood. (f) A variant of this scenario involves sequential generations, rather than sequential stages within an individual. Many invertebrates require several sequential generations to complete their annual life cycle, for example, the annual emergence of sexual or winged propagation stages or the annual emergence of migratory phenotypes in butterflies. Although the mechanistic basis of such multiple-generation life cycle is poorly known, each individual and each generation possess the entire genomic repertoire that is needed for the complete, annual rhythm; image: Edda Starck

## 26.6 Adaptive Significance of Circannual Clocks

The functional significance of entrained biological rhythms under natural conditions is well understood. Demonstrating the functional significance of their endogenous component is proving more difficult because biological rhythms strongly interact with surrounding environmental factors, but recent studies have provided important insights [24, 44]. For circannual rhythms, their wide taxonomic spread, the broad scope of processes that are under their regulation, and the differences between closely related taxa suggest a major functional role under natural conditions. Their adaptive significance is strongly suggested by at least two features of circannual rhythms:

The first critical feature of circannual timekeeping is its predictive power to anticipate and prepare for upcoming seasonal changes in the environment (cf. Sect. 1). In a highly seasonal habitat, where changes in food supply and other selective pressures can be predicted through photoperiod, the timing mechanism allows for very precise regulation of the timing of cycles in physiology and behaviour. The anticipatory mechanism allows timing to be planned much in advance of the ecological events that ultimately determine survival and reproductive success. For example, in red deer (*Cervus elaphus*), the separate events of the seasonal cycle must be integrated to produce births at an optimal time in the spring. This optimal timing is determined by the availability of food to the mothers to lactate the offspring and also by direct effects of environmental conditions on the calves [45, 46]. It has been demonstrated that young being born too early in the spring die of immediate effects of the hostile environment, while those being born too late in the spring die in their first winter, having failed to grow adequately during the summer. For the parents to achieve this timing, all the events across the entire year must be co-ordinated. Regulation of appetite, food intake, accumulation of fat reserves and the development of the appropriate pelage and of antlers and other secondary sexual characteristics all need to be timed by an inherent timing mechanism. In seasonal habitats where photoperiodic changes are small, populations often nonetheless show robust annual cycles, which however may differ between neighbouring populations [5]. For example, rufous-collared sparrows (*Zonotrichia capensis*) on the western and eastern slope of the Andes have robust breeding cycles that are out of phase, and these two neighbouring populations have reduced gene exchange [47]. - Low-amplitude photoperiod conditions also facilitate asynchronous cyclicality of individuals within a population (polymorphisms, Figs. 26.4b and 26.5b; see below). Finally, when seasonal changes are unpredictable, the timing mechanism allows for more flexible regulation of physiology and behaviour. For example, finches on the Galapagos Islands appear to be in a constant state of partial reproductive activation, allowing them to rapidly initiate breeding during vegetation flushes after the scarce rains [48].

Second, circannual timekeeping allows organisms to express robust annual cycles which at specific phases override the effects of proximate cues, including

photoperiod. A classical example is cross-equatorial migratory birds that traverse across hemisphere and thus experience long-day conditions in winter as well as in summer. Similarly, hibernating species may spend many months under constant darkness but arouse on time for vegetation regrowth in spring. Yet another example is high Arctic species, where the organisms are enabled to tolerate the continuous light of summer, and continuous darkness of winter, when regulating their annual rhythms. In such cases, the inertia of the endogenous component continues to drive the rhythm, and its phase-specific response mechanism enables eventual synchronisation to the zeitgebers during highly selective times of year [33].

Species differ in their responsiveness to immediate environmental conditions relative to reliance on internal timekeeping mechanisms. Reliance on endogenous features safeguards against being misled by untimely cues, such as unseasonal weather, but this advantage must be carefully balanced against benefits of direct responses to the environment. Such interspecific differences are highly relevant as environmental conditions are being rapidly altered under climate change [49, 50].

## 26.7 Variation in Circannual Timekeeping

Species and populations vary remarkably in the fine-tuning of seasonal timekeeping, depending on habitat and life history [7]. Species differ in the particular time of year at which a given behaviour, such as breeding, occurs. In some cases these differences can be explained by specific life histories, such as winter breeding of birds that have specialised on conifer mast that becomes available in winter (crossbills [12]). In other cases, social reasons, for example, competition over breeding or feeding opportunities, can lead to staggered life cycle timing. An impressive example of this is the sequential use of island habitat by sympatrically breeding seabirds, which has been associated with allochronic speciation [51]. Based on related observations on a circadian timescale, researchers have introduced the idea that time, like space, may be partitioned as an ecological resource [52]. We propose that the idea of a temporal niche applies likewise on an annual timescale.

Furthermore, within populations, there is variation between individuals in the exact timing of seasonal events, such as the onset of breeding or the onset of migration, with some being early relative to the population average and others being late [53–55]. To the extent that such polymorphisms in annual timing are consistent over several years, individuals can be seen to possess specific, annual ‘chronotypes’. This is analogous to the daily chronotypes described in circadian biology [56, 57]. Such variation is particularly large in environments that are conducive to year-round seasonal activities like reproduction. In contrast, reproductive timing of organisms at high latitudes can often be synchronous to within a few days [4]. Whatever the relative magnitude of such individual differences, they

provide opportunities for partitioning of time as an ecological resource. This is illustrated by the asynchronous musth cycles of Amboseli elephant bulls (Fig. 26.5b), which reduce male-male confrontation and allow males to maximise mating opportunities. Time-dependent reproductive success and mortality have also been demonstrated in birds living at higher latitudes [46, 55]. We propose that an individual's chronotype can function as a temporal equivalent to a spatial territory and suggest the use of 'time territory' to describe this feature of biological timekeeping. Assuming that chronotype is heritable, it can be predicted that this will accelerate evolutionary change in timing programmes, as appears to occur in allochronically breeding seabirds [51].

Finally, even within a single organism, different seasonal processes, such as moult and gonadal development, can vary independently, due to the separate physiological regulation described above [10, 35]. As a consequence, a species can modify the timing of one process without necessarily modifying the timing of another. This promotes the evolutionary potential of circannual phenotypes and determines species adaptability to environmental change [50].

## 26.8 Gwinner's Synthesis: 30 Years Ago

Eberhard Gwinner (Fig. 26.7) was particularly interested in the environmental control and ecological significance of endogenous annual rhythms (migratory warblers, European starling, African stonechat). In 1986 he published a synthesis of the current literature entitled *Circannual Rhythms: Endogenous Annual Clocks*



**Fig. 26.7** Ebo Gwinner's synthesis. Professor Eberhard Gwinner (Ebo) was director of the Max-Planck Institute of Behavioural Physiology (subsequently, Ornithology) at Erling-Andechs in Germany. He had worked there from 1964 until his untimely death in 2004, investigating circannual and circadian rhythms in passerine birds

*in the Organization of Seasonal Processes*. This demonstrated unequivocally the universal importance of circannual timing mechanisms across organisms from all taxa – plants, insects, birds, mammals and even unicells. The formal properties of circannual timing, with parallels to circadian timing, were thereby defined and have since then been confirmed, elaborated and extended:

1. *Robustness*: Circannual rhythms, like circadian rhythms, continue in total isolation from environmental rhythmicity.
2. *Innateness*: Circannual rhythms, like circadian rhythms, are endogenous (self-sustained and innate) and continue throughout the life cycle.
3. *Free-running period*: Compared to circadian rhythms, the range of free-running periods and the extent of inter- and intra-individual variation are larger in circannual rhythms.
4. *Temperature compensation*: Period length of circannual rhythms, like that of circadian rhythms, is largely unaffected by temperature, although evidence is still scarce.
5. *Entrainment*: Circannual rhythms, like circadian rhythms, entrain to zeitgebers, are particularly responsive to photic cues and may involve transients.
6. *Permissive conditions*: The light conditions under which circannual rhythms are expressed are more variable than those of circadian rhythms.
7. *Zeitgeber properties*: The zeitgeber properties under which circannual rhythms entrain are generally more variable than those of circadian rhythms (e.g. range of entrainment, zeitgeber amplitude).
8. *Independence*: Circannual rhythms cannot be explained by frequency demultiplication of circadian rhythms.
9. *Interaction with the circadian system*: The circadian system may contribute to circannual rhythm regulation through annually changing external and internal coincidence or simply through measuring day length. An impaired circadian system does not necessarily disrupt circannual rhythmicity (e.g. SCN-lesioned mammals, pineal-ectomised birds, Arctic damping of clock gene expression).
10. *Broad regulatory scope*: Circannual rhythms, like circadian rhythms, regulate many processes, including alternation between active and inactive phases.
11. *Taxonomic spread*: Circannual rhythms, similar to circadian rhythms, are taxonomically widespread.
12. *Evolutionary lability*: Differences between closely related species suggest that circannual rhythms, like circadian rhythms, are under selection and have high potential for evolutionary change.

## 26.9 Onward Journey: Future of Circannual Studies

Research on circannual rhythms is now at an exciting stage and is beginning to reveal underlying physiological mechanisms (Chaps. 26–31, [10, 58]). This is largely thanks to the revolution in DNA sequencing techniques that can potentially identify all genes in a species' genome that change transcription

across the circannual cycle, and these can then be classified into biological pathways. This may allow the final identification of a cohort of circannual genes, analogous to the canonical circadian clock genes that by interaction generate circannual time. Species-specific molecular tools are also available to measure the chronological changes in gene expression across long-term transitions in physiology. In situ hybridisation and other methodologies are being used extensively to localise the seasonal events within different tissues.

A remarkably wide spectrum of plant and animal models that express annual timing are also now available to be investigated. This includes the detailed genetic characterisation of growth and flowering in the model plant, *Arabidopsis* (Chap. 29). Use of this model is revealing the way epigenetic control of specific ontogenetic genes determines long-term timing processes. There is also a new focus on single-cell organisms, including *Alexandrium* sp., based on the premise that this may reveal the molecular basis of a circannual clock system that is cell autonomous (Chap. 29). At an ecological and evolutionary level, major advances in our understanding of the adaptive significance of circannual timing are predicted. This can involve sampling individuals repeatedly through the annual cycle, at different stages of the compartmentalised life history as in insects and/or across a series of generations [59]. It is probable that information on circannual phase is transferred across generations through the epigenetic modification of gene function (Chap. 29). Plasticity in timekeeping within and between closely related species is also a striking feature in nature which needs to be more fully explored [49]. Such research should reveal the subtle interactions between the internalised clockwork and external environment cues. These may come from climatic features, food quality, the presence of a mate and a plethora of other signals that govern timing on a local ecological scale.

Finally, there is an increasing awareness that circannual biology is of economic and medical relevance to humans. Increasing our understanding of annual cycles in farm animals, family pets and wild species is required to help answer many animal welfare and conservation issues. This is of major current interest because of concern about the unknown impact of rapid climate change, for example, the worrying effects of increasing temperature on the ecology of insects that act as vectors for disease [50]. There are also lessons to be learned from species that show profound seasonal cycles in physiology and behaviour. For example, hibernating mammals utilise a flexible adjustment of insulin resistance to progressively regulate the seasonal change from an obese state at the onset of winter to a life-threatening emaciated state by spring [60]. This may help understand why modern lifestyles that overcome winter deprivation are causing the current human epidemic of obesity and diabetes.

Overall, we emphasise that circannual timing mechanisms are universal. Evolution has operated in a seasonally periodic world throughout Earth's long history, and as a consequence, innate timing processes that predict this periodicity are found in all taxa from unicells to elephants. We now know that humans themselves are no exception – we are a far more seasonal species than previously assumed. In a recent genome-wide screen, using human white blood cells and adipose tissue, a high

proportion of genes were found to change their expression between spring, summer, autumn and winter. This was the case in humans from different ethnic groups and from highly industrialised human societies [50, 61]. Studies of other primates have also revealed that the basic mechanisms of circannual rhythmicity are present in the primate lineage [62]. There can be no doubt ancestral circannual clocks continue to tick in us in still unexplored ways and significantly affect contemporary human life.

### Synthesis

After several decades of working in the field of seasonal timing, we highlight the following key points:

1. When a seasonal cycle is observed in any organism, it is most likely to be regulated by an *endogenous timing mechanism* rather than by the changing environment. Natural selection for ‘optimal timing’ operates over countless generations to produce clockwork mechanisms that anticipate the cyclical environment.
2. Responses to photoperiod are *not an essential* requirement for the expression of endogenous circannual rhythms, and moreover, these can obscure insights of the underlying timing process. The past emphasis on characterising the mechanisms of photoperiodic time measurement has distracted from the attempts to resolving the genetic basis of endogenous circannual timing.
3. Circannual rhythms are expressed at the level of the *individual* – due to genetic control. They need to be studied by repeated measurements on known individuals (marked, known ID) across at least two complete circannual cycles. If individuals vary in their cycles (time or amplitude), then population studies are useless at revealing rhythmicity. This applies notably to species that have evolved in equatorial regions, including humans.
4. Within individuals, different circannual processes can become uncoupled from each other, indicating that circannual rhythms consist of independent, *modular components* (e.g. moult, reproductive cycles) and do not result from a sequence of interconnected life cycle stages.
5. In species with a compartmentalised life history, as in insects, the circannual clock *resides permissively* in all stages but may be phenotypically expressed only once in development, e.g. eclosion. The expression of circannual timing can also be *transgenerational*, e.g. where a species undergoes a series of generations across the year.
6. Circannual organisms express *annual chronotypes* (e.g. differences in phase and/or magnitude of their long-term rhythms), analogous to the way circadian organisms express daily chronotypes (e.g. ‘larks and owls’). This polymorphism potentially exapts a species to climate change because some seasonal phenotypes will prosper, presumably altering the associated gene frequencies for the circannual timer genes.
7. Just as territorial animals occupy *physical space* to protect food supply and mates (favouring survival and reproductive success), so can an organism occupy *seasonal time space* to be more competitive.
8. Overall, good timing is *adaptive*.

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