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REVIEW

Biological timekeeping in polar environments: lessons from terrestrial vertebrates

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ABSTRACT

The polar regions receive less solar energy than anywhere else on Earth, with the greatest year-round variation in daily light exposure; this produces highly seasonal environments, with short summers and long, cold winters. Polar environments are also characterised by a reduced daily amplitude of solar illumination. This is obvious around the solstices, when the Sun remains continuously above (polar 'day') or below (polar 'night') the horizon. Even at the solstices, however, light levels and spectral composition vary on a diel basis. These features raise interesting questions about polar biological timekeeping from the perspectives of function and causal mechanism. Functionally, to what extent are evolutionary drivers for circadian timekeeping maintained in polar environments, and how does this depend on physiology and life history? Mechanistically, how does polar solar illumination affect core daily or seasonal timekeeping and light entrainment? In birds and mammals, answers to these questions diverge widely between species, depending on physiology and bioenergetic constraints. In the high Arctic, photic cues can maintain circadian synchrony in some species, even in the polar summer. Under these conditions, timer systems may be refined to exploit polar cues. In other instances, temporal organisation may cease to be dominated by the circadian clock. Although the drive for seasonal synchronisation is strong in polar species, reliance on innate long-term (circannual) timer mechanisms varies. This variation reflects differing year-round access to photic cues. Polar chronobiology is a productive area for exploring the adaptive evolution of daily and seasonal timekeeping, with many outstanding areas for further investigation.

KEY WORDS: Polar, Seasonal, Circadian, Circannual, Chronobiology, Arctic, Phenology, Photoperiodism

Introduction

Solar cycles driving polar biological rhythms

The Earth is approximately spherical; therefore, the intensity of solar radiation reaching its surface declines with latitude (Fig. 1A); hence, it is colder in the polar regions than at the Equator. Because the axis of the Earth's daily rotation is tilted ~23 degrees relative to the plane of orbit around the Sun, there is an annual cycle of daily insolation (i.e. energy input/unit area in a 24 h period), the amplitude of which is strongest in the polar regions (Fig. 1B,C). Conversely, the daily cycle of solar elevation declines in amplitude as one moves from the Equator to the poles (Fig. 1D). This is most obvious around the

solstices at latitudes in excess of 66°N/S (Fig. 1E), which experience at least one day each year when the Sun does not set (polar day) and one day a year when the Sun does not rise (polar night). This latitudinal definition of the polar regions contrasts with other working definitions (e.g. the 10°C summer isotherm; Blix, 2005), and focuses attention on the polar light environment.

Low-amplitude rhythms of daily illumination present opportunities and challenges for animals living in the polar regions. For example, during the polar day, there is the opportunity for diurnal species to remain continuously active for extended periods, whereas the same light conditions limit foraging opportunity for nocturnal species. There is wide variation in daily behavioural patterns in polar species: some species adhere to daily patterns of behaviour, whereas others adopt activity patterns that are continuous or ultradian (see Glossary).

The high-amplitude annual cycle of solar insolation in polar regions results in strong environmental seasonality, characterised by short, intense summer growing seasons separated by long, cold winters. Thus, all animals exploiting the polar regions must meet a seasonal energy challenge. They do so through strong seasonal programmes of physiological and behavioural adaptation, allowing exploitation of summer feeding opportunities and mitigation against winter energy demands.

Chronobiology for innate control of temporal organisation

The field of chronobiology deals with internal timekeeping processes through which daily and seasonal temporal synchrony is maintained (Dunlap et al., 2004). Timekeeping involves three connected elements (Fig. 2A): sensory systems that take cues from the environment (especially light cues) for use as synchronising signals or 'zeitgebers' (see Glossary); core timer systems, which sustain 'free-running' rhythms (see Glossary) in the absence of zeitgebers; and output pathways connecting timers to physiology and behaviour. Modern circadian chronobiology can be traced to a set of 'empirical generalisations about circadian rhythms' defined by Pittendrigh (1960), still accepted some six decades on. Pittendrigh (1960) identified temperature-compensated (see Glossary), self-sustained, free-running rhythmicity with a period of approximately 24 h (circadian; from the Latin *circa dies*; see Glossary) as a key innate feature, widely observed in living organisms.

To investigate the properties of timekeeping elements, chronobiologists have developed experimental paradigms using highly unnatural lighting regimes (Fig. 2B). These include continuous illumination/darkness to reveal innate oscillatory characteristics; square wave on–off light–dark transitions applied at different periodicities to explore how core oscillators (see Glossary) couple to the external 24 h day, and 'skeleton photoperiods' (see Glossary) used to define the importance of light–dark transitions in entrainment (see Glossary). This toolbox has powered our understanding of biological timekeeping and has led to the wide acceptance of a non-parametric model for daily

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Glossary
Definitions are adapted from the Dictionary of Circadian Physiology (www.circadian.org/dictionary.html).

Aschoff's rule
This rule states that the endogenous free-running circadian period (tau, τ), observed in constant darkness (DD), will shorten for diurnal animals and lengthen for nocturnal animals when they are exposed to constant light (LL).

Circadian
Occurring or functioning in cycles of approximately 24 h. For most researchers, the definition of circadian requires endogenous generation (as determined by the ability to free run under constant conditions). Some researchers make the additional demand that a circadian rhythm is entrainable by a zeitgeber with a period in the circadian range (approximately 19–28 h).

Circannual
Occurring or functioning in cycles of approximately one year. For most researchers of biological rhythms, the definition of circannual must include the requirement of endogenous generation (as determined by the ability to free run under constant conditions): this is type 2 circannual rhythmicity as defined by Goldman in Dunlap et al. (2004). Accordingly, the use of the term circannual in connection with annual rhythms whose endogenous nature has not been ascertained is acceptable only if there is a justifiable assumption of endogenesis. Some researchers make the additional demand that a circannual rhythm be entrainable by a zeitgeber with a period in the circannual range (approximately 8–16 months).

Diel
Having the duration of a day (24 h).

Entrainment
The synchronisation of a self-sustaining oscillation (such as a circadian rhythm) by a forcing oscillation (the zeitgeber). Under conditions of steady entrainment, the period of the self-sustaining oscillation conforms to that of the zeitgeber, and there is a stable phase relationship between the two.

Free-running
The state of a self-sustaining oscillation (rhythm) in the absence of effective zeitgebers or other environmental agents that may affect the period of the oscillation.

Oscillator
A functional entity capable of generating spontaneous rhythms.

Photoperiodism
The response of an organism to changes in day length (photoperiod).

Skeleton photoperiod
A light–dark cycle whose photophase consists of two brief episodes of light exposure per cycle.

Subjective day
The segment of a circadian cycle during the free-running state that corresponds to the illuminated segment during entrainment by a light–dark cycle.

Subjective night
The segment of a circadian cycle during the free-running state that corresponds to the dark segment during entrainment by a light–dark cycle.

Temperature compensation
The property of preserving the rate of a biological process as the surrounding temperature changes.

Ultradian
Occurring or functioning with a frequency higher than circadian.

Zeitgeber
A synchronising agent (a stimulus capable of resetting a pacemaker or synchronising a self-sustaining oscillation).

synchronisation of circadian systems (see Box 1; Pittendrigh and Daan, 1976b) and day length (photoperiod) measurement (Pittendrigh and Daan, 1976a). This model performs very well in many settings; alternative, possibly superior, models that emphasise chronic effects of light exposure as well as light–dark or dark–light transitions have not yet been generally adopted (Roenneberg et al., 2010) (see Box 1).

Despite its merits, the non-parametric model places emphasis on light–dark/dark–light transitions, which contributes to the misapprehension that animals living through the polar night and the polar day are free running, in a natural version of the constant conditions used by chronobiologists. This is too simplistic: even at the summer solstice in the high Arctic, changes in solar elevation maintain a daily cycle of light intensity (Fig. 1E). Additionally, the daily cycle of solar position interacts with local topography (e.g. sea cliffs; Huffeldt et al., 2020) to produce pronounced daily cycles of sunlight/shade; this is potentially compounded by animal behaviour (e.g. individuals may retreat into burrows; Hut et al., 1999) to produce higher-amplitude daily cycles in light exposure than otherwise expected. Furthermore, the spectral composition of light depends on solar elevation, particularly when the Sun is close to the horizon (Fig. 1F,G), providing further time-of-day information. Accordingly, studies in mice provide direct evidence for colour as an entraining signal (Mouland et al., 2019; Walmsley et al., 2015). Hence, although the disappearance of dawn/dusk transitions in the midsummer and midwinter periods is the defining feature of the polar regions, it does not follow that polar animals lack light-based time of day or photoperiodic information at these times.

The polar setting poses interesting chronobiological questions. What determines whether a given polar species maintains daily synchrony year round? In species that show year-round daily synchrony, how is this achieved? In species that break away from 24 h periodicity in daily patterning, what happens to the core timer and its coupling to output pathways? At the annual time scale, do polar animals depend on the same day length-sensing systems as temperate seasonal species, and how are these systems specialised to cope when dawn and dusk transitions disappear? By addressing these questions, polar chronobiology offers insights into mechanistic relationships between light and biological clocks, and into the evolution of biological clock mechanisms. At an applied level, understanding seasonal timekeeping in Arctic species may help mitigate against climate change-driven changes in phenology, while understanding the effects of light at night in wild species adapted to prolonged natural darkness may help reduce the effects of human Arctic colonisation.

In this Review, we focus on terrestrial vertebrates biologically adapted to polar environments; we exclude humans because of the profound complicating effects of technological adaptation in this species. Even within this restricted group, the body of laboratory work on biological timekeeping in polar species is patchy, limiting our capacity to test chronobiological formalisms. Indeed, there is a recent preponderance of field-based studies within which it is impossible to discriminate diel organisation (see Glossary) in the presence of zeitgebers from true circadian rhythmicity, which involves free-running organisation under constant conditions (and a failure to acknowledge this fact). Attributing observations of weak (i.e. low-amplitude or dampened) circadian rhythmicity to polar adaptation often appears to be a form of confirmation bias, occurring without reference to comparable temperate species. We suggest that a framework considering the ultimate bioenergetic drivers for temporal organisation and recognising the necessity for controlled light experiments to define the role of innate timers is the only effective way to navigate the extant literature and to structure future research programmes in polar chronobiology.

We first consider circadian organisation, before shifting to circannual rhythms and photoperiodism (see Glossary). For both
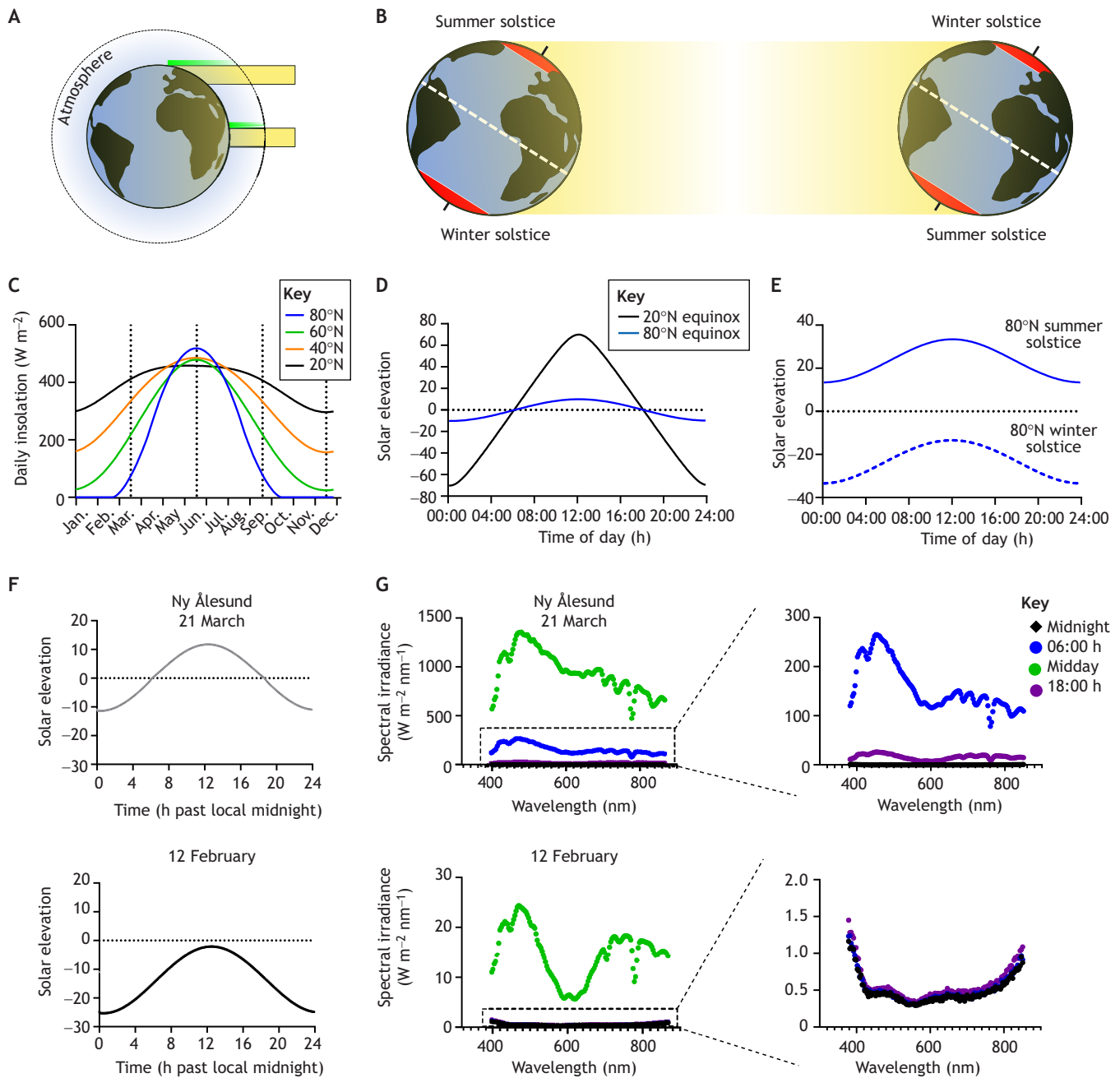
Fig. 1. The polar light environment. (A) Solar radiation reaches the polar regions at an oblique angle, increasing the distance of travel through the atmosphere and reducing irradiance intensity. (B) The tilt of the Earth's axis leads to a strong annual cycle of insolation, the amplitude of which increases with latitude (C). (D) There is a reduced amplitude of daily cycles of solar elevation in the polar regions, where the Sun is continuously above or below the horizon at the solstices (E). Data are from the NOAA solar calculator. (F,G) Solar elevation compared with all-sky spectral composition in Ny Ålesund (78°N). Data are shown for 21 March and 12 February, during the polar night. Note that on 12 February, the spectral composition is relatively bluer than at the equinox. Data kindly provided by Tomasz Piotr Kopec, UiT.

areas, we start with a survey of the literature describing formal time-keeping properties based on organism-level behavioural and physiological monitoring before considering the state of knowledge regarding the underlying molecular physiological mechanisms.

Circadian organisation
Circadian activity patterns in Arctic animals
In 1960, questions regarding the possible existence and biological function of circadian rhythms in Arctic organisms were already on

the agenda; Pittendrigh (1960) noted that it was unclear whether animals living in the Arctic were exposed to sufficiently strong daily zeitgebers to maintain circadian entrainment, or whether adaptation to Arctic life removed the selection pressures under which circadian organisation evolved. Below, we assess how far we have progressed from these reflections on Arctic circadian biology. We do not aim to review all observations of activity patterns in polar animals; rather, we focus primarily on those studies including controlled experiments to evaluate circadian characteristics.
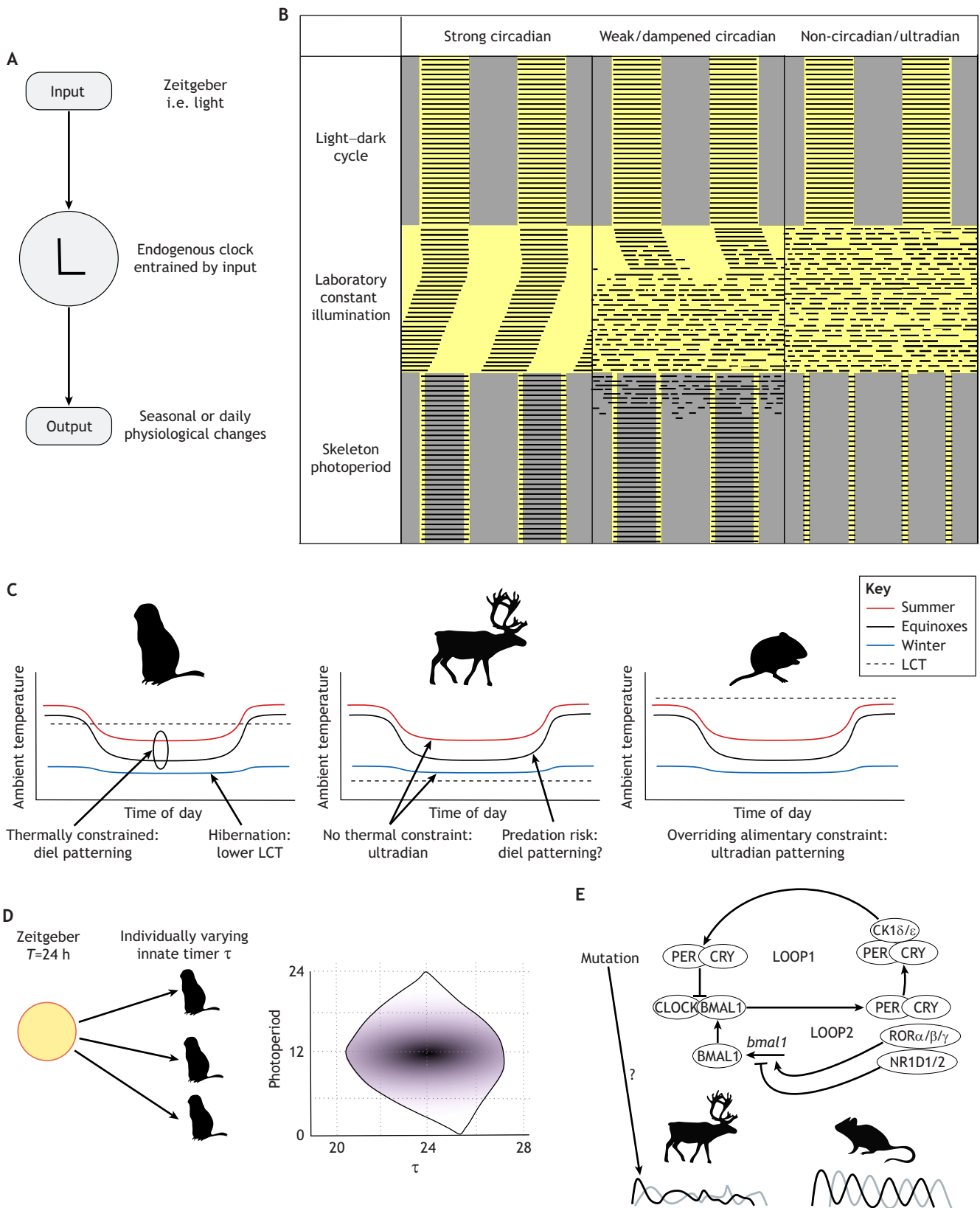
Fig. 2. See next page for legend.

Rodents

Pittendrigh's student Richard Swade studied locomotor activity in Arctic rodents, combining field observations with trapping data and controlled experiments on wild-captured animals (Swade and Pittendrigh, 1967). Swade observed notable species differences in the persistence of daily organisation of activity among Arctic rodents.

Fig. 2. Polar perspectives on circadian organisation. (A) Circadian clocks are entrained to the solar day by zeitgebers, especially light. The clock drives daily and seasonal changes in physiology/behaviour through neural and endocrine output pathways. (B) Schematic actograms showing how responses of a diurnally active animal to artificial lighting reveal circadian organisation. Horizontal lines indicate bouts of activity on successive days. Two successive 24 h periods are shown for each actogram. Under constant illumination, strongly circadian organisms show robust free-running rhythms. Rhythms break down where circadian organisation is weaker. Skeleton photoperiods maintain entrainment in circadian organisms but elicit a masking response, i.e. the environmental light level directly drives the behavioural response, in non-circadian organisms. (C) Patterns of temporal organisation predicted by a circadian thermo-energetic framework (Hut et al., 2012; van der Vinne et al., 2014). In the summer, arctic ground squirrels (left) experience environmental temperatures below their lower critical temperature (LCT) each day, favouring circadian-driven withdrawal into burrows when solar elevation falls. Arctic reindeer (middle) experience temperatures above their LCT even in the polar night, relaxing the thermo-energetic drive for circadian patterning. Weak diel patterning at the equinoxes may reflect crepuscular predation risk. In voles (right), alimentary constraints lead to ultradian patterning year round, even in environments with a strong diel cycle in ambient temperature. (D) Period alignment to cope with polar zeitgebers. Redrawn based on Schmal et al. (2020). Individual variation in circadian period (τ) leads to variable capacity to entrain to long or short photoperiods. This yields an onion-shaped envelope for entrainment limits, where the breadth at a given photoperiod (y-axis) represents the range of values of τ that can entrain to an environmental period (T) of 24 h. (E) A schematic diagram of the circadian molecular clockwork in mammals. In reindeer, lack of selective pressure to maintain circadian organisation may have been responsible for mutations in the per2 gene. The grey and black lines represent the oscillation of per2 and bmal1 genes, respectively, in fibroblast culture (based on Lu et al., 2010).

In Arctic ground squirrels (*Urocitellus paryii*, formerly *Spermophilus paryii*), daily activity is centred on midday in the field even in high summer; this is matched by robust circadian patterns of wheel running in captive animals exposed to constant light. Subsequent observations of circadian organisation in free-living Arctic ground squirrels strongly confirm these observations (Williams et al., 2012a,b, 2017a) and also show that recovery of circadian organisation after the hibernation season is enhanced by renewed exposure to the daily solar illumination cycle (Williams et al., 2017a).

Box 1. Circadian entrainment

The mechanisms underlying the synchronization of clocks by light cues have been discussed since the establishment of chronobiology as a discipline (see Daan, 2000; Tackenberg et al., 2017). Historically, two models of entrainment have been proposed: In the 'parametric' or 'continuous' entrainment model, the light intensity continuously modulates the clock speed by accelerating or decelerating passage through a limit cycle, and this leads to a sustained (tonic) adjustment of the clock phase to the natural cycle. The 'parametric' nomenclature is because the effects of light require a change in at least one of the oscillator parameters (Aschoff et al., 1971; Daan, 2000; Roenneberg et al., 2010; Tackenberg et al., 2017). In the 'non-parametric' or 'discrete' entrainment model, light is proposed to cause a rapid change to clock phase (phase shift), and the magnitude of this change is dependent upon when in terms of internal ('subjective') clock time the light exposure occurs. Light exposure around 'subjective dawn' advances the circadian clock, whereas light exposure around 'subjective dusk' serves to delay the clock. Smaller phase shifting effects occur during the middle of the 'subjective day' or 'subjective night' (see Glossary). The resulting effect is that light-resetting effects around dawn and/or dusk are particularly important for circadian entrainment to the solar light–dark cycle (Daan, 2000; Pittendrigh, 1960; Roenneberg et al., 2010; Tackenberg et al., 2017).

In contrast, tundra voles (*Alexandromys oeconomus* previously known as *Microtus oeconomus*) trapped at Arctic locations in Alaska reveal no evidence of 24 h rhythmicity at the summer solstice, while outdoor-housed wild individuals only resume a nocturnal pattern in August (Swade and Pittendrigh, 1967). This solstitial loss of daily rhythmicity is also seen in red-backed voles (*Clethrionomys rutilus*), while singing voles (*Microtus miurus*) show individual variability in their response to solstitial conditions (Swade and Pittendrigh, 1967).

None of the above necessarily reflects adaptation to life under Arctic illumination: Swade and Pittendrigh (1967) also explored the effects of translocating a southern species of ground squirrel – the antelope ground squirrel (*Ammospermophilus leucurus*) – to Alaska, and found that this species maintains daily entrainment at the Arctic summer solstice, similar to the Arctic ground squirrel. The loss and restoration of circadian organisation as a consequence of hibernation is also seen in temperate species of ground squirrel. Weak diel patterning and a propensity towards ultradian activity is a feature of temperate vole species, including *A. oeconomus* (Halle, 1995). Hence, Arctic rodents do not necessarily lose or maintain diel synchrony under a weak zeitgeber, or exhibit robust or decayed intrinsic circadian entrainment; interspecific differences seen in the Arctic mirror those seen at temperate latitudes.

Large mammals

Here, we consider large mammals to include species for which body mass exceeds 10 kg. There are no published data from controlled experiments designed to determine whether any Arctic ungulate exhibits intrinsic circadian rhythmicity. Activity rhythms in high Arctic-resident (78°N) Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and in their counterparts (*R. tarandus tarandus*) in Tromsø, north Norway (70°N) have been recorded (van Oort et al., 2005, 2007). In both subspecies, Arctic summer and Arctic winter are associated with loss of diel organisation, and this is more pronounced in Svalbard, where no statistically significant diel patterning is observed. More recently, Arnold et al. (2018) used a similar approach to look at activity, heart rate and rumen temperature in Svalbard reindeer; they concluded that there is persistent diel organisation throughout the polar summer. Although they term this organisation 'circadian', no animals were held under the constant conditions required to determine innate circadian rhythmicity. Rather, the authors' inference of 'circadian' stems from detection of periodicity in their activity data, with a period length not statistically different from 24 h, and therefore indistinguishable from diel patterning. In fact, the strongest feature of activity patterns presented in this study is ultradian rhythmicity, entirely consistent with the earlier work of van Oort and colleagues (2005, 2007).

Recently, studies of activity patterns in free-ranging Greenland muskoxen (*Ovibos moschatus*; van Beest et al., 2020), wolverines (*Gulo gulo*; Thiel et al., 2019) and lynx (*Lynx lynx*; Heurich et al., 2014) reported 'circadian' rhythms of activity or body temperature, which were strongest around the equinoxes. However, as for the reindeer studies, no assessments under constant conditions were undertaken, and in the solstitial phases, continuous or ultradian activity patterning dominates. Ultradian activity patterning is a characteristic shared with ungulates living at lower latitudes (Berry et al., 1982; Owen–Smith and Goodall, 2014), probably reflecting the dominant effect of ruminant metabolism on behaviour patterns (Hazlerigg and Tyler, 2019).

Year-round monitoring of polar bear (*Ursus maritimus*) activity in northern Alaska by a combination of GPS and accelerometry

shows diel organisation, even during the Arctic summer and winter (Ware et al., 2020). Contrary to the authors' assertion that bears remain rhythmic 'even during periods of constant conditions', this study presents no data collected under constant conditions, and therefore none of the rhythmicity can be considered 'circadian' *sensu strictu*. Measured period lengths do not diverge significantly from 24 h, although during the Arctic summer there is a tendency for the measured period to be slightly longer (up to 24.5 h, see figure 5 in Ware et al., 2020) than it is around the equinoxes. This may reflect a long-period circadian oscillator struggling to entrain to a weak 24 h zeitgeber or possible tidal influences on foraging behaviour; the data collected cannot be used to assess whether circadian rhythms are free running. Overall, data on polar bears show no clear departure from data on brown bears (*Ursus arctos*; Thiel et al., 2022; Ware et al., 2012), and they maintain diel synchrony through the Arctic summer. We cannot draw any strong inferences about the characteristics of presumptive underlying circadian oscillators.

Birds

Field observations of diel behavioural patterning are available for a variety of shore birds and other summer visitors to the polar regions [e.g. Steiger et al., 2013; Daan and Tinbergen, 1979; Huffeldt et al., 2020; Eichhorn et al., 2021 (in which behaviour is incorrectly termed 'circadian')]. These show that behavioural activity can remain synchronised to the solar day (period length not significantly different from 24 h) or become essentially continuous. Interestingly, biparental nest attendance can give rise to rhythmical patterns of activity that appear quasi-circadian (Bulla et al., 2015; Cresswell et al., 2003; Steiger et al., 2013), but the observed duration of activity depends on the length of time each parent sits on the nest; therefore, the available data can also be interpreted as the result of two coupled interval timers.

In the Alaskan summer, Lapland longspurs (*Calcarius lapponicus*) remain synchronised to the solar day; in light-controlled aviaries, they express free-running circadian activity (Ashley et al., 2014), which – in agreement with Aschoff's rule (see Glossary) (Aschoff, 1960) – is slightly shorter in birds held in constant light (23 h) than in constant dark (23.7 h). Other lab-based studies on the summer visitors to the Arctic (i.e. snow buntings and bramblings) show that they can entrain to alternating cycles of colour/spectral composition (Pohl, 1999) and to the relative position of an orbiting light source (Krüll, 1976a). However, Lapland longspurs do not entrain to diel changes in light intensity or colour (Ashley et al., 2014). It has also been noted that the strength of the zeitgeber (position or colour) in the absence of a light intensity cycle appears to vary with seasonal reproductive status (Krüll, 1976a; Krüll et al., 1985). Clearly, there is considerable scope for further studies to refine our understanding of the capacity of passerine birds to find circadian zeitgebers during the polar summer.

The only Arctic resident bird to have been subjected to controlled lighting experiments is the Svalbard ptarmigan (*Lagopus muta hyperborea*). In birds held on a natural Arctic photoperiod, the diurnal activity seen around the equinoxes disappears around the solstices (Stokkan et al., 1986). Under artificial light–dark cycles, Svalbard ptarmigan express diurnal activity and body temperature (T_b) cycles, and both activity and T_b show clear anticipatory increases prior to the lights-on signal (Appenroth et al., 2021b). Direct switches from light–dark cycles into either constant bright light or constant darkness lead to rapid breakdown of activity rhythms but gradual dampening of T_b rhythms in ptarmigan (Hofinger, 2021). Overall, these studies suggest that Svalbard ptarmigan possess a dampened circadian timer, which allows non-diel organisation to dominate around the solstices.

Willow ptarmigan (*Lagopus lagopus*; which are closely related to Svalbard ptarmigan) born in Northern Alaska (68–69°N) and held at 64°N under natural light conditions show similar 'continuous' activity during the 'near' polar summer (West, 1968). Although comparable studies on temperate ptarmigan species (*Lagopus lagopus* and *Lagopus muta* spp.) are lacking, it seems plausible that during the polar day and polar night, the escape from circadian dominance into a more flexible around-the-clock foraging behaviour is beneficial for Arctic and sub-Arctic grouse species.

Interpreting daily activity patterns through a circadian thermo-energetic framework

The circadian thermo-energetic (CTE) hypothesis states that circadian control of daily patterns of activity and rest manages the trade-off between intake and expenditure of energy (Hut et al., 2012; van der Vinne et al., 2014). Accordingly, withdrawal into insulative nests at night minimises thermoregulatory costs during the coldest part of the daily cycle, while thermoregulatory costs of feeding are lowest in the warmer daytime phase. The key assumption is that for part of the day, ambient temperature (T_a) falls below the lower critical temperature (LCT) for thermoneutrality (i.e. the range of temperatures within which energy expenditure is not required to maintain homeothermy). Because the LCT for small rodents is generally higher than T_a in the Arctic (Riek and Geiser, 2013), this assumption generally holds in Arctic settings.

How then, do behaviour patterns in Arctic mammals align with the CTE hypothesis? To answer this, it is necessary to consider thermal energy constraints under field conditions. Studies using Arctic ground squirrel pelt 'mannequins' to assess 'effective environmental temperature' (T_e, a measure factoring moisture and wind speed into the estimation of temperature-dependent energy dissipation), concluded that, even in the Arctic mid-summer, surface conditions periodically fall below LCT for approximately 8 h every day (Long et al., 2005). Hence, in the Arctic ground squirrel, the observed diurnality and nocturnal withdrawal, even in the Arctic summer, can be seen as predictable when considering the CTE framework. By contrast, the LCT of the Svalbard reindeer remains well below 0°C even when in summer pelage (Nilssen et al., 1984); thus, the CTE framework predicts no diurnal constraint for this species, and continuous (ultradian) activity throughout the 24 h cycle becomes a favourable strategy (Hazlerigg and Tyler, 2019) (Fig. 2C).

The maintenance of robust entrained rhythmicity implies that circadian machinery must be preserved, as seen in robustly rhythmic rodent species at lower latitudes. Arctic species that maintain robust entrained rhythmicity must also be sensitive to the low-amplitude daily cycle of solar light intensity that these animals experience. In this regard, the use of burrows for withdrawal in the 'subjective night' may serve to amplify the intensity of the signal to maintain circadian resonance. It is also possible that, in some smaller Arctic species, bioenergetic (CTE) constraints driving the maintenance of entrainment under a weakened photic zeitgeber may influence the characteristics of the core circadian machinery. In this regard, Schmal et al. (2020) offer a strong theoretical treatment of relationships between internal oscillator characteristics and duration of the external photoperiod. They predict that, for the polar regions, as the photoperiod tends towards the polar day or the polar night, circadian entrainment can only be maintained if the innate free-running oscillator period tends towards 24 h (Fig. 2D). In other words, resonance between the internal biological oscillator

and the environmental cues signalling the 24 h period becomes increasingly important for circadian synchrony in the polar solstitial phases.

Arctic ground squirrels showing diel synchrony during the polar summer struggle to maintain synchrony when placed on artificial square-wave photoperiods, but nevertheless maintain activity rhythms with periods close to 24 h (Williams et al., 2017b). Although this is broadly consistent with predictions of the Schmal model (Schmal et al., 2020), it appears that in both Arctic and European ground squirrels (Hut et al., 1999), changes in solar light quality while animals are out of their burrows are critical for maintaining synchrony. Further theoretical and experimental work is required to define the extent to which changes in total irradiance or spectral composition act as zeitgebers in these species.

Molecular circadian clocks in Arctic animals

Circadian rhythms emerge from cell-autonomous transcriptional/translational negative-feedback loops (TTFLs; Takahashi, 2017). In mammals and birds, key components of the primary negative-feedback loop are the transactivating proteins Clock and Bmal1, and the transcriptional repressors Period (PER) and cryptochrome (CRY). Clock–Bmal1 heterodimers promote transcription of PER and CRY through E-box DNA response elements, while PER–CRY heterodimers repress Clock–Bmal1 actions (Fig. 2E). Protein degradation of PER and CRY proteins by E3 ubiquitin ligases contributes to the emergence of transcriptional oscillations from this feedback cycle. A secondary negative TTFL involving the nuclear hormone receptors Rev-erb alpha and retinoic acid receptor-related orphan receptors (ROR homologues) controls the transcription of genes with ROR DNA response elements (RORE), including Bmal1. These loops modulate cellular physiology through large numbers of clock-controlled genes that contain E-box elements or RORE in their promoter regions but do not feed back on TTFL function. In mammals, circadian rhythms are ultimately synchronised by a master clock located in the suprachiasmatic nucleus (SCN; Hastings et al., 2018). In contrast, birds apparently rely on a clock network involving the retina, pineal gland and SCN (Cassone and Menaker, 1984; Gwinner and Brandstatter, 2001).

In the context of Arctic species, the molecular circadian clock has been described in Svalbard ptarmigan, Lapland longspurs, Arctic ground squirrels and reindeer (Appenroth et al., 2021a; Ashley et al., 2014; Hofinger, 2021; Ikeno et al., 2017; Lin et al., 2019; Lu et al., 2010). In Svalbard ptarmigan, clock gene expression in the mediobasal hypothalamus and pituitary is rhythmic under a light–dark cycle and persists following transfer to constant light (Appenroth et al., 2021a), supporting a typical role for circadian organisation in tissues important for photoperiodic timekeeping. Lapland longspurs also show persistent rhythms in per2 mRNA expression within the eye (an avian master clock) for at least 48 h after transfer to constant conditions, consistent with the conserved rhythmic expression of per2 seen in other vertebrates (Ashley et al., 2014). In Arctic ground squirrels, PER2 immunoreactivity in the SCN shows a 24 h rhythm in animals held under a light–dark cycle, but not in hibernating animals kept in constant darkness (Ikeno et al., 2017). This probably reflects the suppressive effect of the hibernation state per se on circadian clock gene rhythms, which has been described previously (Revel et al., 2007).

In contrast to the Arctic birds investigated, the molecular circadian clock of the reindeer is reportedly weakened or absent (Lu et al., 2010), as shown using luciferase reporter experiments in reindeer skin fibroblasts (Fig. 2E). bmal1- and per2-promoter reporter constructs reveal robust circadian transcription in mouse fibroblasts, whereas in reindeer fibroblasts, low-amplitude rhythmicity is dampened within 2–3 cycles (Lu et al., 2010). The basis for the weak circadian clock in reindeer has been suggested to be a reindeer-specific mutation in the core clock gene per2 (P1172T), which reduces PER2 affinity for CRY1 (Lin et al., 2019). These observations are not conclusive, however. The promoters used by Lu et al. (2010) were based on the mouse per2 and bmal1 genes and may not faithfully report on transcriptional rhythms in reindeer fibroblasts. Direct tests of the consequences of the P1172 T mutation for circadian oscillation have not been undertaken. Finally, it is possible that a 'weak' circadian system is a feature of ungulates in general; therefore, until studies on other ungulates are undertaken, this possibility cannot be excluded.

Overall, the persistence and dominance of circadian rhythms in the Arctic broadly reflects what is observed in related temperate species and is species specific. There is no clear evidence that the molecular clockwork is 'inoperable' in polar settings. Thus, the polar environment provides the opportunity to understand the limits of entrainment of circadian systems and to understand how, even under the polar night and day, entrainment can endure in some species. The key to this may be daily changes in the spectral composition of light (intensity, colour), as indicated in some bird species (Krüll, 1976b; Pohl, 1999) and lab mice (Mouland et al., 2019; Walmsley et al., 2015), but more studies in polar species are required.

Photoperiodism and circannual organisation in Arctic species
Eco-evolutionary drivers for circannual organisation and photoperiodism

In his comprehensive analysis of the ecophysiology of reproduction, Bronson (1989) summarised two major alternative strategies for matching seasonal breeding to environmental energy supply: 'opportunism' – where the decision to breed reflects a direct response to current energy availability as a driver – and the 'predictor option', where the decision to breed is based on predictions of energy conditions over the forthcoming months. Surveying different mammalian groups, Bronson (1989) showed that use of the predictor option increases with latitude (i.e. it is associated with predictable seasonality) and in species with higher longevity (Fig. 3A). A striking demonstration of the predictor option is seen in the seasonal breeding patterns of deer species from different latitudes held at 51°N in London Zoo (Lincoln, 1985). Here, despite year-round access to favourable nutrition and housing conditions, a clear cline based on native latitude is observed, with a narrowly constrained season in northern species (including reindeer) and year-round breeding in southern variants (including axis and sambar deer).

The observation of prediction or anticipation suggests innate timing; indeed, in many species, there is evidence of a circannual timer, analogous to a circadian timer, which persists in the absence of external synchronising cues (Gwinner, 1986). The annual cycle in the daily pattern of solar illumination (photoperiod) is the key cue used to synchronise circannually timed processes to the annual environmental cycle, a phenomenon known as 'photoperiodism' (Baker and Ranson, 1932; Marshall, 1936). Therefore, the predictor option allows organisms to exploit photoperiod to synchronise internal circannual programmes of physiological change so that appropriate seasonal phenotypes (i.e. breeding, fattening, over-wintering, white pelage/plumage) are expressed at appropriate phases of the solar year.
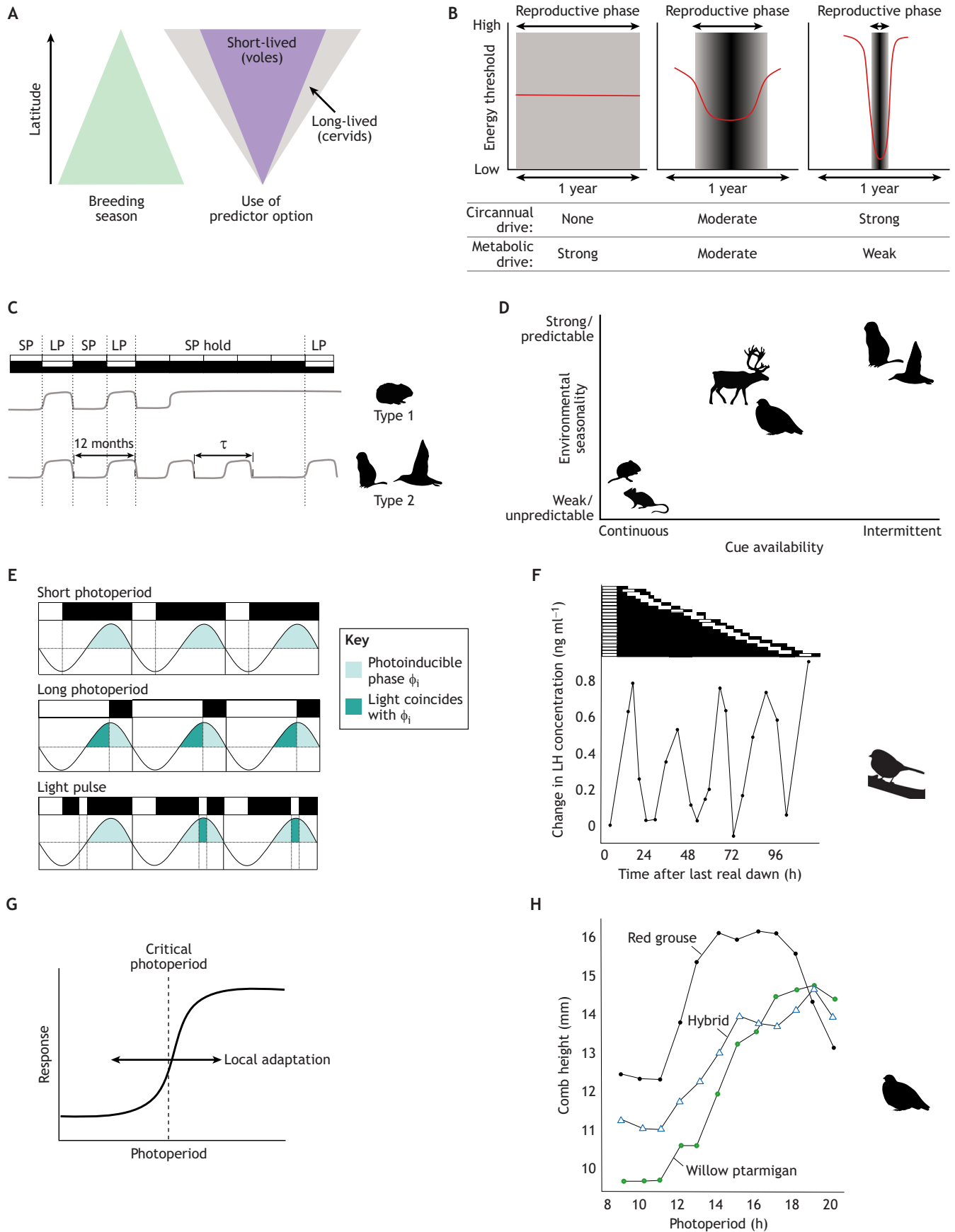
Fig. 3. See next page for legend.

Fig. 3. Polar perspectives on circannual organisation. (A) Effect of latitude on seasonal temporal organisation (Bronson, 1989). As latitude increases, the length of the breeding season decreases (green triangle) and the use of the predictor option increases (purple and grey triangles). The purple triangle represents short-lived species, e.g. voles. The grey triangle represents long-lived species, e.g. cervids. (B) Seasonal gating of reproduction by a circannually programmed energy threshold. In opportunistic species, breeding can occur at any point in the year, provided energy requirements for breeding exceed an internally defined threshold (red line). In circannual species, the internal threshold for reproduction becomes permissive in a limited time window. The slope linking low (permissive) and high (restrictive) levels for the internal threshold defines seasonal plasticity (faded shading) in response to yearly variation in energy supply. (C) Contrast between type 1 (photoperiod sustained, e.g. ptarmigan, Syrian hamster) and type 2 (self-sustained, e.g. golden mantled ground squirrel, red knot) circannual rhythmicity. τ is the free-running period of the circannual rhythm. SP, short photoperiod; LP, long photoperiod. (D) Relationship between circannual cue availability, environmental seasonality and seasonal breeding strategy. Continuous cues and weakly seasonal environments favour opportunistic breeding. Strong predictable seasonality, combined with intermittent cue availability (migration/hibernation), favours type 2 circannual rhythmicity. (E) Coincidence timer model for photoperiodic time measurement, based on Bünning (1960). A circadian rhythm in light sensitivity, represented as a sinusoidal waveform, generates a 'photoinducible phase' (ϕ_i, pale teal shading), during which exposure to light provokes a long-day response. Exposure to a 24 h light–dark cycle with a short photoperiod (top) or long photoperiod (middle) synchronises the circadian rhythm of light sensitivity to produce different photoperiodic responses. Under short photoperiod, exposure to light does not coincide with ϕ_i, and short-day physiology is maintained. Under long photoperiod, light coincides with ϕ_i (dark teal shading), stimulating a long-day photoperiodic response. An artificial discontinuous photoperiod including a 'light break' (bottom) can trigger a long-day response by coincidence with ϕ_i. (F) Example of a light-break experiment in white-crowned sparrows (redrawn based on Follett et al., 1974). A series of different light treatments are shown in which a light break (white rectangles) is applied at progressively longer intervals after 'dawn' (the start of the first light bar in each row). Note how the corresponding reproductive response (plasma concentration of luteinising hormone, LH) changes periodically through the different protocols. This reflects the light break moving in and out of phase with ϕ_i as described E. (G) Local evolution of the critical photoperiod response. (H) Evidence for heritable variation in critical photoperiod from cross-breeding between ptarmigan sub-species (redrawn based on Sharp and Moss, 1981).

Even in species that rely on photoperiodism for annual synchronisation, current energy status can modulate expression of the seasonal phenotype. This is clearly shown for reproductive maturation in sheep, where nutrition in the juvenile phase modulates whether the onset of puberty occurs in late summer or autumn, and can even delay puberty by a full year to the second autumn of life (Foster et al., 1985). Hence, for seasonal breeding, a continuum exists between fully opportunistic breeding and a fully photoperiodic predictor option. This can be visualised as an energy status threshold that may change over the course of the year (Fig. 3B). Where the threshold is constant throughout the year (Fig. 3B, left), animals are fully opportunistic breeders, whereas a square-wave function would represent a rigidly deterministic photoperiodic predictor (Fig. 3B, right). For most species, including those in the Arctic, it is realistic to expect that this function would have a progressive waveform (Fig. 3B, centre), particularly for those phases of the year when phenotypic transitions take place. Hence, the steepness of the slope function represents the degree to which the circannual programme permits plastic timing in the expression of seasonal phenotype.

Formal properties of circannual timer systems and entrainment by photoperiod

Circannual programmes differ between species in the extent to which they progress through complete cycles in the absence of external synchronising cues. Type 1 circannual rhythms (e.g. seasonal breeding in Syrian hamsters) require photoperiodic input for complete cycles of the circannual programme to continue; in contrast, type 2 circannual rhythms continue independently of photoperiodic change and use photoperiodic change as a zeitgeber to maintain synchrony with the solar year (Fig. 3C; Dunlap et al., 2004). Examples of type 2 rhythms include the hibernation cycles of some species of ground squirrel and chipmunk (Pengelley et al., 1976), and moult, body mass and gonadal status in red knots (Piersma et al., 2008). Experiments to define the properties of circannual rhythms, including possible type 2 rhythmicity, require animals to be held under constant photoperiods for long durations (i.e. years), and expression of endogenous rhythms may depend on the fixed photoperiod to which individuals are exposed (Gwinner, 1986); there is therefore a much sparser literature on this topic than on circadian rhythms.

Fig. 3D considers how the strength of environmental seasonality and the availability of photoperiodic cues shape the evolution of type 1 or type 2 circannual rhythmicity. Type 2 circannual rhythms appear to be a feature of organisms that exploit highly seasonally predictable environments, but that seasonally withdraw from these environments, generating photoperiodic discontinuity. For example, withdrawal may happen through either hibernation or translatitudinal migration, both of which are discussed below. A further possibility is that – even for resident year-round active Arctic species, e.g. Svalbard reindeer – type 2 timing is favoured because of weak photoperiodic information in the solstitial phases.

Photoperiodism

Whether animals exhibit type 1 or type 2 circannual rhythmicity, a general expectation is that photoperiodic synchronisation depends on a circadian-based mechanism for measurement of day length (often called the Bünning Hypothesis; Saunders, 2005). Stemming from seminal work by Bünning (1960), the concept is that photoperiodic timers interpret day length through a circadian rhythm of photoinducibility. According to this model, light has two effects: (1) it synchronises the circadian system, and (2) if it is present during the 'photoinducible phase' (ϕ_i), it directly stimulates a long-day response (Fig. 3E). Because the photoperiodic response depends on whether light coincides with ϕ_i, this is known as a coincidence timer model, variants of which have been discussed extensively elsewhere (Goldman, 2001; Pittendrigh and Daan, 1976a).

Several formal approaches have been developed to test the involvement of coincidence timing, and these generally involve use of short light pulses ('light break experiments'; Bünning, 1960) or non-24 h photoperiodic cycles (Nanda and Hamner, 1958) to reveal circadian rhythms of photoinducibility (Fig. 3E). These approaches have been used in a wide variety of birds (e.g. quail: Follett and Sharp, 1969; whited crowned sparrow: Follett et al., 1974; Fig. 3F) and mammals (e.g. Syrian hamster: Elliott et al., 1972; sheep: Ravault and Ortavant, 1977) from temperate latitudes, and they consistently support the involvement of circadian coincidence timing in photoperiodic time measurement. Whether this also applies to Arctic species is presently unknown, and attempts to use the necessary formal approaches have only been undertaken in the Svalbard ptarmigan (Appenroth et al., 2021a).

Photoperiodic responsiveness may be quantified using experimental assessment of a parameter known as critical photoperiod, defined as the photoperiod necessary to stimulate a specified seasonal response (e.g. the photoperiod above which a bird in winter condition is stimulated to reactivate the gonadal axis). In practice, definition of the critical photoperiod requires that

responses to a range of photoperiods are measured, so that the photoperiod necessary for a half-maximal response can be calculated; this is effectively a photoperiod dose–response analysis (Fig. 3G). Theoretical consideration of temperature–photoperiod relationships (Bradshaw and Holzapfel, 2007; Hut et al., 2013) predicts that critical photoperiod will increase with latitude. Critical photoperiod analyses require large numbers of individuals and may be confounded by issues of photoperiodic history. This means that the body of experimental literature on this subject is dominated by studies of insect diapause; these studies generally show increases in critical photoperiod with latitude (Bradshaw, 1976; Lehmann et al., 2015; Tauber and Tauber, 1972). For mammals and birds with distributions extending into the Arctic, we are aware of only three studies from which it is possible to make critical photoperiod estimates: one on tundra voles (van Delum et al., 2023) and two on ptarmigan (Appenroth et al., 2021a; Sharp and Moss, 1981; Fig. 3H).

Neuroendocrine mechanisms of the photoperiodic response

In the last three decades, the study of photoperiodic control of reproduction has seen extensive progress in defining the neural pathways connecting opsin-based photoreception to seasonal changes in endocrine regulation, and hence to the seasonal phenotype (Hazlerigg and Simonneaux, 2015). In mammals, night-time production of melatonin by the pineal gland relays the photoperiodic signal to the pars tuberalis (PT, part of the pituitary gland; Fig. 4A). Melatonin-dependent production of thyrotropin by PT cells (Hanon et al., 2008; Ono et al., 2008) then drives alterations in thyroid hormone conversion in the adjacent tanycytes of the hypothalamus, leading to seasonally altered autonomic and reproductive endocrine outputs. The mechanism in birds is also PT–tanycyte based (Nakao et al., 2008), but here the photoperiodic message is thought to reach the PT via opsin photoreceptors in the diencephalon (Davies et al., 2012; García-Fernández et al., 2015; Halford et al., 2009; Nakane et al., 2010, 2014). The same pathway is also linked to seasonal body weight changes and the expression of torpor in mammals (Murphy et al., 2012). Seasonal control of prolactin secretion – and hence the pelage mammalian cycle – occurs through a less well-defined intra-pituitary mechanism (Lincoln and Clarke, 1994).

The melatonin dependence of photoperiodism in mammals links daily (circadian) and annual (circannual) synchronisation, and this is emphasised by considering the molecular pathways within the PT controlling production of thyroid-stimulating hormone (TSH): melatonin acts through transcriptional control loops involving canonical clock genes (*per*, *cry*) and clock-controlled genes (e.g. *tef*, *dec1*) and associated co-activators (EYA3; Dardente et al., 2010; Masumoto et al., 2010; Wood et al., 2015, 2020; Fig. 4B,C).

Our understanding of the mechanisms described above comes from studies of domesticated lab-amenable species native to temperate latitudes (sheep, hamsters and Japanese quail) chosen for their strong expression of photoperiodic responses. This leaves many unanswered questions. For example, how do photoperiodic synchronisation and circannual timing mechanisms operate in wild species? By what mechanism are photoperiodic cues integrated with other signals such as food availability and temperature? Below, we summarise knowledge on these topics from an Arctic perspective.

Arctic mammals

Although there has been extensive observation of strong seasonality in the field across muskoxen, reindeer, Arctic ground squirrels,

Arctic rodents and polar bears (e.g. Flood and Tedesco, 1997; Leader-Williams, 1988; Ramsay and Stirling, 1986; Sheriff et al., 2011; Stevenson et al., 2009), experimental studies exploring innate circannual timing are generally lacking. A recent exception is a study on Arctic ground squirrels, which explored spontaneous exit from hibernation under controlled constant conditions (Chmura et al., 2022). This was paralleled by spontaneous changes in TSH and hypothalamic deiodinase gene expression in the PT during the hibernation season, as seen in earlier studies in circannually hibernating European hamsters (Sáenz de Miera et al., 2014). Given that temperate ground squirrel species show strong type 2 circannual rhythms in body weight, hibernation and reproductive activation (Pengelley et al., 1976), the available data suggest that Arctic ground squirrels express type 2 circannual rhythms under PT–tanycytic control.

Experimental exploration of photoperiodic influences on seasonal physiology has been undertaken in one other Arctic mammal, the reindeer (Hazlerigg et al., 2017). Although this species remains active year round, and breeds in the autumn, it undergoes a pronounced seasonal cycle of body fattening and voluntary food intake, with the latter reaching a nadir in mid-winter. When reindeer are brought indoors and transferred to constant darkness or constant light, they undergo an accelerated increase in food intake, moult and antler development compared with animals kept on a simulated natural photoperiod (Hazlerigg et al., 2017). This effect might be due to an escape from the delaying effects of short photoperiod exposure. The melatonin profile in reindeer under natural photoperiods shows a clear night-time peak of secretion at the equinoxes, but in the Arctic summer and winter, melatonin secretion becomes continuous (Stokkan et al., 2007); moreover, melatonin secretion appears to be directly light responsive, as opposed to a circadian output signal (Lu et al., 2010). These results suggest that synchronising effects of melatonin on circannual physiology mainly occur in the spring or autumn equinoctial phases. Programmed melatonin infusion experiments in pinealectomised sheep demonstrate that artificial melatonin signals representing only 3 month segments of the year-round signal can act as circannual zeitgebers (Woodfill et al., 1994; Fig. 4C). We speculate that analogous mechanisms in reindeer and muskoxen (Tedesco et al., 1992) maintain year-round seasonal synchrony.

Birds

Photoperiodic effects on seasonal traits have been studied in three distinct groups of polar birds: year-round Arctic residents (willow ptarmigan and Svalbard ptarmigan: Appenroth et al., 2020, 2021a; Stokkan and Sharp, 1980; Stokkan et al., 1982, 1986), long distance trans-latitudinal migrants that breed in the Arctic (the red knot: Piersma et al., 2008) and passerines whose summer breeding range extends northwards into the Arctic (the common redpoll and the white-crowned sparrow: Hahn et al., 2004). For the passerines, the Arctic represents a northward extension of a high-temperate breeding range, whereas, in the case of red knots, summer breeding involves a long-distance translocation to the Arctic light environment.

In ptarmigan, exposure to increasing photoperiods or transfer to constant light initiates a summer programme (plumage change, reproductive activation and loss of body fatness; Sharp and Moss, 1981). This is followed by spontaneous progression to an autumn programme (reproductive inactivation, moult, body fattening), even if exposure to long photoperiods continues (Stokkan et al., 1982). This phenomenon of 'photorefactoriness' develops at shorter photoperiods in temperate red grouse than in Arctic willow
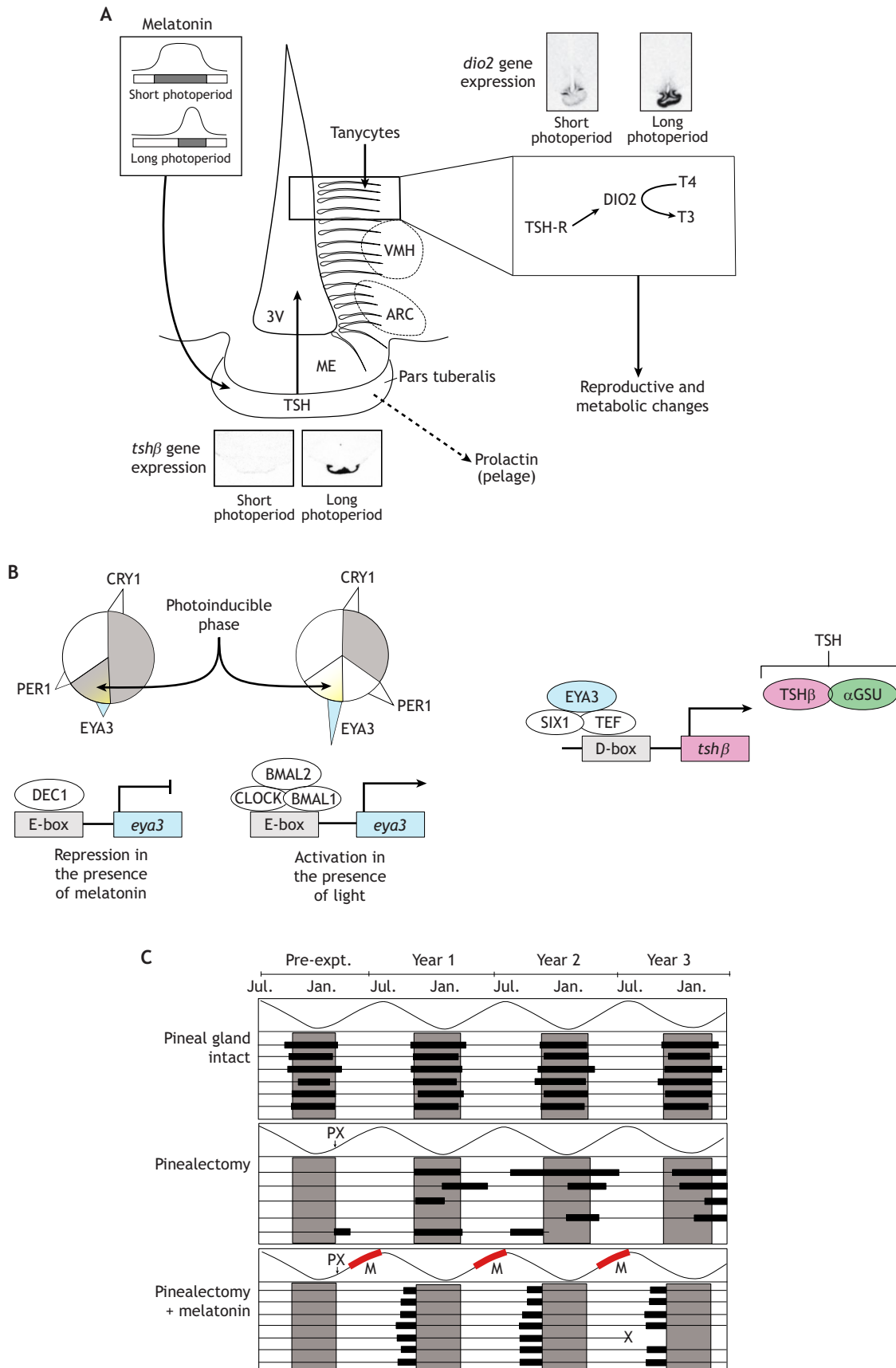
Fig. 4. See next page for legend.

Fig. 4. Substrates for the synchronisation of circannual rhythms.
(A) Model for seasonal synchronisation through the hypothalamo-pituitary complex. In both birds and mammals, photoperiodic information is processed in the pars tuberalis of the pituitary, leading to daylength-dependent production of thyrotropin (TSH). See text for details. The figure includes *in situ* hybridisation images for *tshβ* and *dio2* gene expression in long and short photoperiod-housed sheep. 3V, 3rd ventricle; ARC, arcuate nucleus; VMH, ventral medial hypothalamus; ME, median eminence; TSH-R, thyrotropin receptor. (B) Model for circadian-based induction of a photoperiodic response within the mammalian pars tuberalis (Dardente et al., 2010; Masumoto et al., 2010; Wood et al., 2020). Left: the circles represent 24 h, white is the light phase and grey is the dark phase. The left circle represents short photoperiod, and the right circle represents long photoperiod. The phase of *cry1* expression in the pars tuberalis is at the onset of darkness, and *per1* expression is induced at the onset of light. The white triangles represent the expression level of *cry1* and *per1*. *eya3* expression is induced on long photoperiods when light is coincident with the photoinducible phase (yellow shading on white background); the level of *eya3* expression is represented by the blue triangle. If it is dark in the photoinducible phase (yellow shading on grey background), EYA3 protein expression is presumed to be low. When light coincides with the photoinducible phase, EYA3 is expressed under the control of CLOCK, BMAL1 and BMAL2. In the presence of melatonin (dark), *eya3* expression is repressed by DEC1. Right: EYA3 along with TEF and SIX1 bind to D-box elements in the *tshβ* gene and co-activate *tshβ* expression. TSH-β protein and α-GSU protein form TSH, which is transported to the tanycytes in the mediobasal hypothalamus. (C) Circannual synchronisation of sheep through partial melatonin signals. Redrawn based on Woodfill et al. (1994). Each panel shows the time of year when ewes are in oestrus (thick horizontal lines) over a 3 year experiment in a natural photoperiod (sine wave). Intact ewes show synchronised breeding, whereas pinealectomised ewes, unable to produce melatonin, show disorganised breeding seasons. Artificial restoration of a melatonin signal (red bar, M) for only 3 months per year restores synchronous breeding. PX, pinealectomy; X, death of animal.

ptarmigan (Stokkan et al., 1982). Exposure to short photoperiods does not appear to accelerate the expression of autumn phenotypic characteristics in ptarmigan, and in Svalbard ptarmigan, the short breeding season ends before any decline in photoperiod. Hence, in ptarmigan, the timing of the summer life-history phase depends on innate timekeeping, which is evolutionarily adapted to Arctic photoperiodic conditions. Ptarmigan can be viewed as a type 1 circannual species, given that ptarmigan held under short photoperiods for extended periods do not spontaneously revert to a spring phenotype (Appenroth et al., 2020; Stokkan, 1979). Nevertheless, exposure to short photoperiods re-establishes sensitivity to photostimulatory long photoperiods. Overall, this pattern of long photoperiod-induced photostimulation followed by photorefractoriness and then maintenance of the winter phenotype and restoration of photoperiodic sensitivity is commonly seen in birds (Sharp, 2005), and is similar to observations made in white-crowned sparrows and redpolls (Hahn et al., 2004).

To our knowledge, only one study reports a quantitative difference in photoperiodic sensitivity in an Arctic resident bird compared with its temperate counterpart (Sharp and Moss, 1981; Fig. 3H). Here, the photoperiodic response of willow ptarmigan from northern Norway (*Lagopus lagopus*) was compared with that of Scottish red grouse (*Lagopus lagopus scotticus*) and with willow ptarmigan–red grouse hybrids. Spring reproductive endocrine characteristics appear at shorter photoperiods in red grouse than in willow ptarmigan, whereas hybrids show intermediate response characteristics. Hence, Arctic adaptation in *Lagopus* appears to include genetic adjustment of the photoperiodic response.

Passerine and galliform birds use a circadian-based system to respond to changes in photoperiod (Sharp, 2005). Skeleton photoperiod experiments in Svalbard ptarmigan, using pre-breeding

behaviour and neuroendocrine gene expression changes as readouts for seasonal phenotype, suggest that this mechanism is also operative in a high-Arctic resident species (Appenroth et al., 2021a). Within the limitations of this work, the critical photoperiod appears to be ~14 h (Appenroth et al., 2021a), i.e. slightly longer than values estimated for red grouse and Norwegian willow ptarmigan (Sharp and Moss, 1981). Overall, the available data offer no evidence for qualitative distinctiveness in the circannual programmes in Arctic-breeding birds compared with their temperate counterparts; nevertheless, the data from ptarmigan species support the idea that quantitative refinement of photostimulatory and photorefractory responses maintain Arctic seasonal synchrony.

Long-distance migratory red knots, which breed in the high Arctic, are noteworthy for their expression of type 2 circannual rhythms in plumage moult and body mass change (Karagicheva et al., 2016; Piersma et al., 2008). In some individuals, high circannual rhythm stability is maintained for over 8 years of exposure to a constant photoperiod and temperature (Piersma et al., 2008). Unusually for type 2 circannual rhythms (Gwinner, 1986), these rhythms are slightly longer than a year, possibly reflecting the extension of spring-to-summer phase processes (e.g. spring weight gain; Karagicheva et al., 2016). Transfer of birds that were held on a cycle of 12 h of light and 12 h of dark conditions (LD 12:12) for 7 years to constant light conditions for 1 year had a highly disruptive effect, effectively blocking the expression of the spring-phase characteristics throughout the period of constant light exposure (Karagicheva et al., 2016). It is difficult to draw strong inferences about the underlying circannual timer function from these remarkable data, but the apparent importance of LD 12:12 for expression of type 2 rhythmicity in red knots echoes the results of studies on passerine species from temperate and tropical latitudes, including starlings and stonechats (Gwinner, 1986).

Conclusions and perspective

Modern comparative chronobiology is concerned with the evolution of timekeeping mechanisms, firmly connecting physiology to ecology. The polar setting is not a natural version of the experimental photoperiod treatments used to reveal innate timer processes, but rather is a light environment that provides special challenges to timer synchronisation, as well as extreme cyclical bioenergetic challenges to survival and reproduction. To fully understand the effects of evolution on innate timers in polar species, it is necessary to take animals out of their natural setting and explore their physiology and behaviour under controlled conditions. This has been done in a very limited number of studies, and the overall impression is that no simple generalisations can be made about the Arctic adaptation of daily or seasonal timer mechanisms. Although it would be interesting to understand the causes of weakened overt circadian rhythmicity and breakdown of diel organisation, the current literature fails to provide definitive explanations for this phenomenon. Even less is known about how daily synchrony during the solstitial periods is maintained in species such as the Arctic ground squirrel, and further work on core oscillator characteristics, spectral effects as zeitgebers and behavioural reinforcement of zeitgeber exposure are all potentially fruitful avenues. Data on seasonal synchronisation mechanisms are extremely limited; generally, it appears that, although current models based on temperate mammals and birds also apply for Arctic species, local adaptation may have increased reliance on innate long-term (circannual) processes to allow animals to cope with weakened seasonal zeitgebers around the solstices. Therefore, polar

chronobiology offers an opportunity to deepen our understanding of how internal timers are synchronised to the environment.

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