

# Persistence, Entrainment, and Function of Circadian Rhythms in Polar Vertebrates

Cory T. Williams,<sup>1</sup> Brian M. Barnes,<sup>2</sup>  
and C. Loren Buck<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Alaska Anchorage, Anchorage, Alaska; and <sup>2</sup>Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska  
clbuck@uaa.alaska.edu

Polar organisms must cope with an environment that periodically lacks the strongest time-giver, or zeitgeber, of circadian organization—robust, cyclical oscillations between light and darkness. We review the factors influencing the persistence of circadian rhythms in polar vertebrates when the light-dark cycle is absent, the likely mechanisms of entrainment that allow some polar vertebrates to remain synchronized with geophysical time, and the adaptive function of maintaining circadian rhythms in such environments.

The rotation of the earth around its axis, once every 24 h, exposes almost all living organisms to highly predictable daily rhythms of light intensity and temperature. Circadian systems, comprised of an endogenous biological clock or a network of clocks, are the principal adaptation to this fundamental element in the temporal structure of the geophysical environment. Circadian clocks enable organisms to anticipate and exploit favorable conditions for daily activities through temporal coordination and phasing of biochemical, physiological, and behavioral processes (39, 137, 140). The adaptive value of these clocks is evidenced by their ubiquity, occurring in all organisms examined to date, from unicellular cyanobacteria to multicellular plants and animals (38, 52, 66).

Although the benefits of maintaining circadian rhythms in an environment with robust daily light/dark (LD) cycles is relatively obvious, it has long been speculated that endogenous rhythms of behavior and physiology on a circadian scale may be of little advantage and possibly even disadvantageous and thus not expressed during the continuous lighting conditions of polar summers and winters (34, 63, 123). Daily rhythms of light intensity persist in polar regions, but transitions between light and dark (e.g., day and night) are absent, and, as latitude increases, there is a corresponding reduction in the amplitude of the rhythm. Given that the LD cycle of day and night is both the primary driver for the emergence and evolution of endogenous clocks (111, 129) and also the ultimate synchronizing agent (zeitgeber) for circadian clocks in free-living organisms (49), several questions emerge related to rhythms of indigenous polar organisms. Do entrained or free-running circadian rhythms persist in the absence of a robust LD cycle? If so, what zeitgeber is used by animals to maintain synchrony with geophysical time? And, importantly, what is the biological significance or

function of maintaining rhythmic expression of physiology and behavior in an environment that no longer cycles between day and night?

Here, we review the responses of resident and migratory polar vertebrates to the yearly intervals of continuous lighting characteristic of polar summers and winters. First, we provide a brief overview of the organization of vertebrate circadian systems. We then discuss the diversity of circadian function that has been uncovered for polar vertebrates, with some species becoming arrhythmic across the polar day and/or polar night, whereas others maintain entrained daily rhythms of behavior throughout the year, and others still that exhibit free-running circadian rhythms with periods that are close, but not equal to, 24 h. We subsequently discuss the primary cues vertebrates likely use to entrain their circadian rhythms to geophysical time in the absence of a LD cycle, and we explore the functional significance of maintaining these rhythms from both a physiological and an ecological standpoint.

## Vertebrate Circadian Systems

Timekeeping by circadian clocks is driven by transcriptional-translational feedback loops, whereby rhythmic expression of clock gene products activates the transcription of other clock-associated genes in cycles of ~24 h. Although the specific transcriptional elements that make up the circadian clock vary across taxonomic groups, the molecular basis of circadian clocks is highly conserved within vertebrates, and circadian clock function is broadly similar (26, 28, 56). Although non-transcriptional components alone are sufficient for circadian clock function (88), transcriptional elements typically play an important role.

Vertebrate circadian systems are comprised of networks of endogenous clocks across organs and tissues synchronized to one another by one or

several “master” circadian clocks (26, 38). Master clocks influence circadian physiology and behavior via neuronal and humoral cues (62, 112) and via the synchronization of peripheral circadian oscillators found throughout the body (23). In mammals, the suprachiasmatic nuclei (SCN) in the hypothalamus houses the master clock responsible for directing the circadian organization of physiology and behavior and synchronizing peripheral oscillators (38). Circadian organization in birds, in contrast, is directed by multiple interacting but dissociated master clocks located in the retinae, pineal, and SCN (26). Similarly, fish are thought to have master clock oscillators located within the retinae, pineal organ, and likely the pre-optic region of the hypothalamus (44), although their role as pacemakers has yet to be established through rigorous experimentation.

Circadian clocks have an intrinsic period that deviates slightly from 24 h and therefore must be entrained by an external zeitgeber to remain in synchrony with geophysical time. Alternation of environmental light and dark is the most potent zeitgeber for the entrainment of circadian master clocks in most species; populations of weakly coupled or noncoupled cells within peripheral clocks found throughout the body are synchronized by humoral and neuronal signals (26, 38, 49). In mammals, SCN-directed rhythms of body temperature of 1–4°C amplitude play a critical role in entraining peripheral oscillators (21, 23). Melatonin, synthesized and released during the night phase by the pineal gland, is an important output of circadian master clocks and acts as one of the primary internal-time givers for peripheral clocks and daily physiological processes (95). As such, measurements of daily variation in circulating levels of plasma melatonin, and to a lesser extent body temperature rhythms, in addition to behavioral rhythms of locomotion, sleep, or eating and drinking, are often used as a proxy for assessing rhythmicity in free-living animals.

## Persistence

It has long been assumed that strongly defined cycles of light/dark, temperature, humidity, and other physical and biotic attributes such as predation pressure within the environment place a premium on consolidating one’s activity during particular phases of the daily cycle (24, 25, 60, 130). Based on this assumption, early chronobiologists speculated that activity rhythms might be absent in animals that occupy natural environments that are aperiodic, or nearly so, such as caves, the deep sea, and polar regions (46, 91, 123). However, early studies of arctic migratory birds revealed that individuals often maintained a rhythm of activity across the polar day, typically characterized by a

quiescent period coincident with the lowest light intensity (34, 75a, 124). It was later discovered that persistence of daily rhythms of behavior was not restricted to migratory species; Adelie penguins (*Pygoscelis adeliae*) indigenous to the Antarctic, for example, maintain daily peaks in feeding activity during winter at latitudes as high as 77°S (83, 115, 136), and arctic ground squirrels (*Urocitellus parryi*) maintain daily above-ground activity rhythms during the arctic summer at latitudes as high as 72°N (47, 72, 77, 123). These findings are notable given what has been observed in captive animals where exposure to constant lighting often disrupts circadian organization, resulting in behavioral arrhythmicity or “splitting” of rhythms of activity and rest (78, 96), likely through the desynchronization of clock neurons (87).

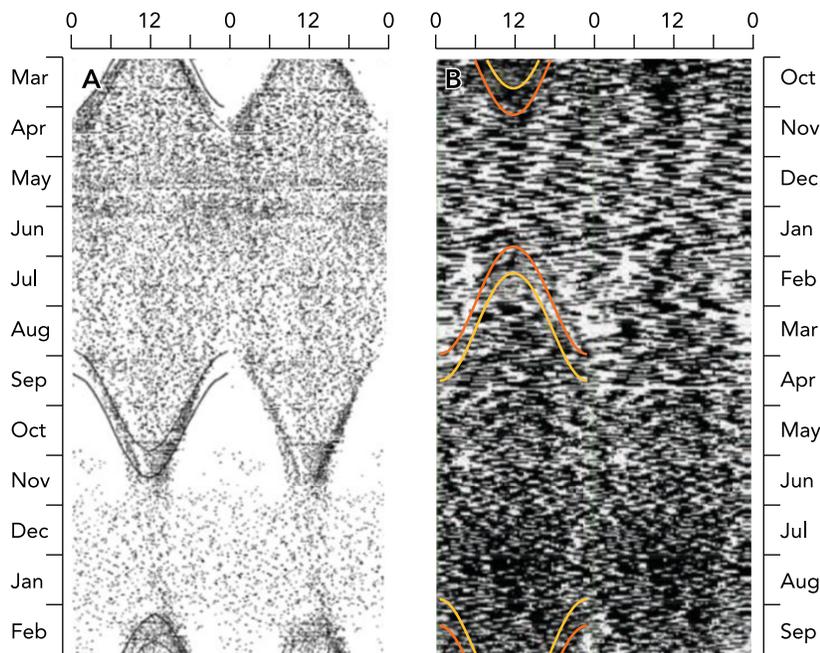
Although early studies reported the presence of daily rhythms in polar vertebrates, subsequent research revealed diverse behavioral responses to the relatively continuous lighting during the polar day and polar night. For example, although Swade and Pittendrigh (123) found that arctic ground squirrels, northern red-backed voles (*Myodes rutilus*), and brown lemmings (*Lemmus trimucronatus*) all exhibit daily rhythms of behavior during the arctic summer, daily activity rhythms were abolished in tundra voles (*Microtus oeconomus*). Some, but not all, of the variation in the persistence of rhythms can be explained by latitude. Daily activity rhythms in captive Svalbard ptarmigan (*Lagopus muta hyperborean*) and free-living arctic reindeer [*Rangifer tarandus tarandus* (70°N) and *R. t. platyrhynchus* (79°N)] were present during the polar night, but not the polar day, at 70°N where significant cycles in civil twilight light intensity continue in winter, whereas activity rhythms were absent during both summer and winter at 79°N (FIGURE 1; Refs. 103, 127, 128). The diel vertical migration (DVM) of polar cod (*Boreogadus saida*) at 70°N stops in late May, coincident with onset of the midnight sun (13). In some fishes, however, activity rhythms will persist during the polar day or night (2, 81).

The occurrence of daily or “diel” (24 h) rhythms of behavior and/or physiology does not necessarily indicate that circadian systems are functional and/or entrained to the natural environment since animals may be responding directly to external cues, a phenomenon known as “masking” (4, 7). Masking behavior itself might also be adaptive, and, therefore, functionality of a rhythm does not necessarily imply that it is endogenously driven. Furthermore, a variety of mechanisms may be responsible for seasonal loss of rhythmicity in behavioral and/or physiological parameters, including the uncoupling of circadian clocks from output pathways, cellular uncoupling resulting in desynchrony of the circadian phase of cells

within circadian clocks, or dampened or arrested oscillations within circadian cells such that clocks can no longer drive output pathways (19). Thus, as with the overt expression of rhythms, the absence of expression of daily rhythms of behavior and physiology in free-living animals exposed to extremes in lighting characteristic of polar environments often may not be indicative of a lack of rhythms within circadian clocks. For example, Steiger et al. (116) recently found that activity patterns of female pectoral sandpipers (*Calidris melanotos*) and male red phalaropes (*Phalaropus fulicarius*) are arrhythmic before incubation, but both groups display daily rhythms of behavior during incubation. Pectoral sandpipers have female-only parental care, whereas red-phalaropes have male-only care; in both species, arrhythmic activity patterns persisted throughout the polar day in the sex that does not care for the young (116). The most parsimonious explanation for the resumption of behavioral rhythms coincident with the onset of incubation in midsummer is that circadian clocks continue to function across the polar day, but clock control of output pathways is plastic and only exerted when it is beneficial to do so. Alter-

natively, rhythmicity may be independent of circadian systems since individuals could be directly responding to lighting conditions, but this masking is only occurring when it is functional.

Although much of the work on circadian rhythms has focused on behavioral rhythms, many studies have also examined physiological parameters that are controlled by circadian clocks, notably patterns of circulating levels of melatonin. Exposure of laboratory animals to constant bright light inhibits pineal function and abolishes circadian rhythms of melatonin production (138). In many arctic and antarctic species, however, melatonin rhythms persist across the polar day [rhythmic melatonin: Adelie penguins (30); Lapland Longspurs (*Calcarius lapponicus*; Refs. 8, 54); willow warbler (*Phylloscopus trochilus*; Ref. 113); Weddell seal (*Leptonychotes weddellii*; Ref. 10)], although findings vary depending on species and in some cases between studies [melatonin not rhythmic: Emperor Penguins (*Aptenodytes forsteri*; Ref. 79); Svalbard ptarmigan (104); Weddell Seal (10); reindeer (42)]. In arctic char (*Salvelinus alpinus*) at 70°N, diel melatonin rhythms persist during the polar night even though lakes have thick ice and



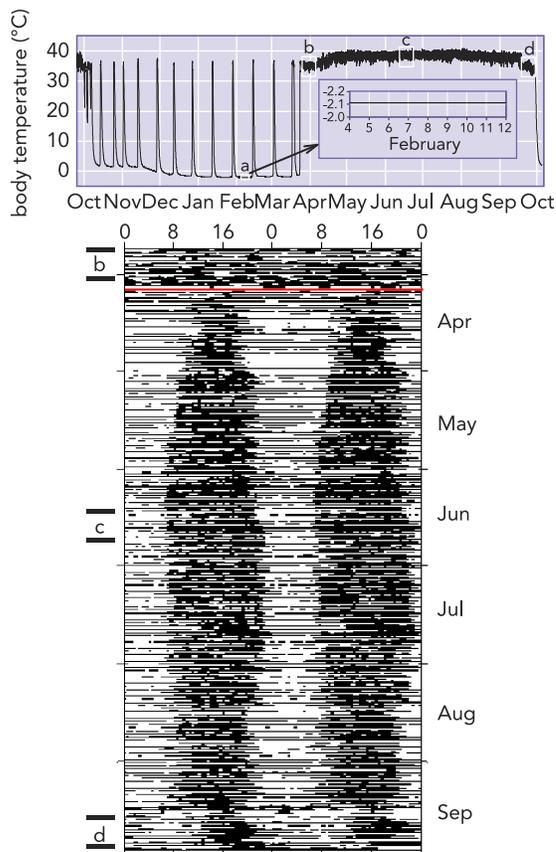
**FIGURE 1. Activity patterns throughout the year** in Svalbard ptarmigan (A) and Svalbard (B) reindeer at 78°N displayed as a double-plotted actograms in which each row represents 2 consecutive days, with bouts of activity (black spaces) interspersed with bouts of inactivity (white spaces). Recorded activity was motion for free-ranging reindeer and feeding behavior for captive ptarmigan. Time of day is indicated above the actogram, and lines drawn on the actogram indicate the start or end of civil twilight (ptarmigan: thick lines; reindeer: orange lines) and sunrise or sunset (ptarmigan: thin solid lines; reindeer: yellow lines). Both species exhibit a seasonal absence of rhythmicity in the circadian range during the polar day and polar night at these latitudes. Reindeer exhibit ultradian rhythms (substantially shorter than 24 h) throughout the year due to alternating bouts of activity and inactivity typical of ruminants. Ptarmigan actogram adapted with permission from Canadian Science Publishing or its licensors (103). Diagram for reindeer adapted with permission from Macmillan Publishers, Ltd. (127).

snow cover; yet, melatonin rhythms are abolished during the polar day (121). However, because light exposure directly inhibits release of melatonin by the pineal, persistent melatonin rhythms could also result from masking.

Melatonin secretion in arctic reindeer, which is only rhythmic during the spring and the fall, appears to be independent of endogenous circadian rhythms and is instead driven predominantly by natural changes in ambient illumination (73, 119). This, coupled with the absence of circadian rhythmicity in two key clock genes within the fibroblast cells of reindeer, led Lu et al. (73) to conclude that the molecular clockwork that drives circadian rhythms may be weak, or absent, in this species, and melatonin-mediated seasonal timing may be more directly driven by photic information at particular times of the year. However, patterns of clock-gene expression within fibroblast cells of reindeer were compared with patterns observed in nocturnal rodents (73) rather than to temperate or tropical ungulates, and therefore it is uncertain as to whether differences in the strength of circadian oscillation reflect adaptation to the arctic environment or are due to differences in taxonomy (i.e., rhythmicity in the expression of circadian clock genes may be generally weaker in ungulates). It is also unclear whether the absence of circadian control and direct sensitivity to illumination observed in melatonin secretion by the reindeer pineal is characteristic of resident polar vertebrates. In fact, it has been argued that in species that exhibit persistent daily rhythms in plasma melatonin levels, endogenous control of melatonin production/secretion within the pineal must be strong to override the suppressive effects bright light typically has on melatonin secretion (30). It is generally assumed that daily rhythms in plasma melatonin levels in polar vertebrates reflect endogenous control rather than responsiveness to subtle changes in the color temperature or intensity of light, although this assertion has rarely been tested directly (but see Ref. 31).

Although melatonin levels are commonly measured to assess rhythmicity, other rhythmically expressed physiological parameters such as body temperature, which acts as a synchronizing agent for peripheral clocks in endotherms (21, 23, 49), can also be useful. Five-month-old captive emperor penguins, for example, do not exhibit daily body temperature rhythms during the constant illumination of summer, but body temperature is rhythmic 6 wk later when 24 h of sunlight persists but daily rhythms in ambient temperature and light intensity are more pronounced (48). In free-living arctic ground squirrels, body temperature rhythms are abolished during hibernation, and the preemergent euthermic intervals of reproductive

males in spring, but daily body temperature rhythms are reestablished coincident with exposure to light and emergence from the hibernacula, and these rhythms persist under the midnight sun (FIGURE 2; Refs. 133, 134). Interestingly, body temperature rhythms of male arctic ground squirrels free run (>24 h) in individuals that are sequestered below ground but euthermic before initiating torpor in autumn (133) strongly suggest that the body temperature rhythm is endogenously driven and not simply a result of masking. Despite the large number of studies on the persistence of physiological and behavioral rhythms in polar vertebrates, we are not aware of a study that has assessed



**FIGURE 2. Annual patterns of core body temperature of a male arctic ground squirrel**  
Annual patterns of core body temperature of a male arctic ground squirrel (top) at 69°N with a double-plotted actogram of when body temperature remained at euthermic levels (i.e., active season; bottom). Each row represents 2 consecutive days of data, with black bars indicating when body temperature was above the mean. Time of day is indicated above the actogram. Body temperature of arctic ground squirrels is constant during deep torpor (a) and arrhythmic during the prolonged interval of euthermic body temperature that occurs in males after heterothermy ends but before they emerge from their burrows (b). Daily rhythms of body temperature are reestablished coincident with emergence from the hibernacula (red line) and persist throughout the active season, including the summer solstice (c). Body temperature rhythms free-run (>24 h) during the below-ground euthermic interval that precedes initiation of torpor in autumn (d). Figure adapted from Ref. 133.

persistence of rhythms at the level of clock gene expression.

### **Temporal Niche Switching**

Animals are generally characterized as diurnal (day active), nocturnal (night active), or crepuscular (twilight active), based on the timing of their daily locomotor activity. Temporal niche switching is a relatively unusual phenomenon in which animals alter their hormonal, physiological, and behavioral rhythms and occupy a different temporal niche without modifying the rhythm of the circadian pacemaker (68). Although the mechanisms that underlie temporal niche switching are not well understood, in at least some species, switching can be induced through food deprivation during the time of day individuals are normally active (59). Interestingly, temporal niche switching has been observed in several polar vertebrates. Freshwater sculpins [Siberian (*Cottus poecilopus*) and European bullhead (*C. gobio*; Ref. 2)] and burbot (*Lota lota*; Refs. 67, 81) at 67°N are diurnal during the spring and fall but become nocturnal during the winter; European bullheads are diurnal during the polar day, whereas both Siberian bullheads and burbot develop asynchronous activity patterns. However, Westin and Aneer (131) found that temporal niche switches in locomotory activity occurred in 4 of 19 fishes studied in subarctic (59°N) aquaria, which suggests this phenomenon may be an adaptation to low ambient lighting conditions during the winter rather than an adaptation to the polar night per se. In mammals, switches from nocturnal wheel-running activity patterns in spring to diurnal activity patterns in summer have been observed in brown lemmings held in captivity at 72°N under natural conditions (123). However, captivity will sometimes induce temporal niche switching in rodents (18, 125), and whether switching occurs in free-living lemmings remains unclear.

## **Entrainment**

### **Light**

Entrainment of circadian rhythms depends on perception of the spectral and spatiotemporal patterns of light, which is influenced by both image (i.e., vision) and non-image forming photoreception. Unfortunately, studies of circadian rhythms in polar animals often report illuminance in lux, a measure of light intensity as perceived by the human visual system and an inaccurate representation of lighting conditions that entrain circadian systems (74). This has important implications for the study of circadian rhythms in polar environments because the amplitude of daily fluctuations in spectral intensity is wavelength-dependent, and daily changes in spectral composition may be more important than changes in light intensity per

se (29, 70, 86, 117). Solar irradiance spectra data, however, reflect radiation incident on a horizontal surface and thus may not be indicative of lighting conditions at the surface where photoreception is occurring (e.g., the retina of the eye in mammals).

Mammalian circadian systems are sensitive to multiple photoreceptive processes, including the melanopsin-driven phototransduction mechanism within intrinsically photosensitive retinal ganglion cells (ipRGCs) expressing the photopigment melanopsin, as well as remote photoreception in rods and cones (15, 51, 100). Recently, melanopic sensitivity functions, in which different wavelengths of light are filtered according to the spectral sensitivity of ipRGCs, have been developed (22, 43), which may provide a more effective means of assessing the changes in light quality and quantity that occur across the polar day that are relevant to mammalian circadian function. However, considerable uncertainty remains in our ability to quantitatively predict how circadian systems will respond to different light exposures reaching the retina (101). A further complicating factor is that circadian systems are influenced by light reception by visual pigments within the retina. This was clearly evidenced by the observation that circadian photoreponsiveness in melanopsin knockout mice is attenuated but not completely lost (89, 107), whereas mice lacking rods, cones, and melanopsin lose all circadian responses to light (53, 90).

The role of light in entraining circadian clocks is more complicated in non-mammalian vertebrates due to the occurrence of complimentary master clocks in the pineal, retina, and SCN (26), the presence of two separate melanopsin pigments (12), and the prevalence of deep-brain photoreceptors that transduce light signals directly to both master and peripheral circadian oscillators (41, 45, 65, 83). However, understanding the importance of deep brain photoreception in maintaining circadian rhythms in an arctic environment is challenging given that sensitivities of deep brain opsins to various wavelengths of light are not well defined. Functionally, it appears as though deep brain opsins and photoreception by the eyes of birds differ in that constant lighting conditions can lead to arrhythmicity, but this effect is not manifest in blinded individuals, which maintain persistent free-running rhythms (41).

The range of wavelengths perceived by an animal's circadian system also depends on pupillary contraction and by transmittance of light through the ocular media. Within mammals, lenses of diurnal sciurid rodents, tree shrews, and primates prevent UV from reaching the retina, whereas lenses among other species exhibit substantial diversity in the degree of short-wavelength transmission (40, 58, 71).

Filtering of UV radiation is notable because rhythms of UV radiation are more pronounced and consistent (less affected by cloud cover) compared with other wavelengths, and peaks in UV radiation tend to coincide with activity (8, 58). Interestingly, in arctic reindeer, the cornea and lens do not filter UV light, and these animals extend their visual range into the UV (57). However, rhythms of behavior within the circadian range are lost in reindeer during both the polar day and the polar night at high latitudes (127, 128). Many birds and nocturnal rodents extend their vision into the UV range, and at least some species can entrain to UV light under laboratory conditions; however, evidence that arctic vertebrates actually use daily cycles in UV light as an entraining agent remains equivocal (9, 40, 58, 98).

Despite widespread taxonomic differences in the mechanisms of light reception in circadian systems, a clear distinction between mammalian and non-mammalian vertebrates in their capacity to entrain circadian rhythms to the polar day and polar night is not evident. We suggest that variation among and within taxa is related to differences in ecological and/or physiological function of rhythms rather than being a manifestation of differences in modes of light reception. Although there is evidence for adaptation of mechanisms of light reception for visual systems in arctic vertebrates (120, 139), we are not aware of any adaptations to the arctic environment in light capture by non-visual circadian systems. However, the discovery of melanopsin pigments, as well as opsins associated with deep brain photoreception, is relatively recent, and this may be a fruitful avenue for future research.

Although subtle diel changes in the intensity and/or spectral composition of light are the most likely cues for entraining circadian rhythms to the polar day, it has also been suggested that the azimuth-position of the sun might be used as a zeitgeber in some polar vertebrates (69, 98). Birds may be the most likely candidate vertebrate species for use of a sun compass as migration routes in at least some arctic birds are consistent with sun compass trajectories (1). Krüll (70) found that captive greenfinches (*Carduelis chloris*) and canaries (*Serinus canaria*) can entrain their activity rhythms to a circling light bulb, providing some support for this hypothesis.

### Nonphotic Entrainment

Light is the dominant zeitgeber responsible for the entrainment of circadian rhythms, and therefore we expect that subtle changes in the intensity and/or spectral composition of light are principally used to entrain polar organisms to geophysical time when a robust LD cycle is not present. How-

ever, other physical and ecological characteristics of the environment are also rhythmic and could act either to entrain circadian clocks or to drive significant physiological or behavioral rhythms through masking. Ambient temperature commonly exhibits diel rhythms in terrestrial polar environments, although whether the predictability of such rhythms or their availability in semi-fossorial species is sufficient to entrain circadian clocks is unclear. Studies of captive non-polar vertebrates indicate that robust diel oscillations in ambient temperature can act as a zeitgeber, although variation in the capacity of individuals to entrain is high (6, 102). Furthermore, although peripheral clocks in endotherms are readily entrained to body temperature, masterclocks are resistant to temperature entrainment and remain phase locked to the light-dark cycle (21, 23). Similarly, patterns of circadian gene expression in peripheral clocks can be phase-shifted in response to temporal feeding restriction under LD or DD conditions, but the phase of circadian gene expression in the SCN is unaffected (36, 118). Thus effects of these nonphotic cues on rhythmicity in polar vertebrates are likely occurring through masking and/or the entrainment of peripheral circadian oscillators. Field and laboratory studies also indicate that the social environment can influence daily and circadian rhythms in numerous species (5, 80, 93), although the mechanisms that underlie social entrainment have yet to be identified.

### Function

It is generally assumed that the adaptive value, or function, of circadian clocks is that they allow organisms to anticipate predictable daily changes in the environment and appropriately adjust timing of their molecular, physiological, and behavioral processes such that they occur at optimal phases of the cycle. Although this concept of functionality has mostly been based on conjecture, recent studies in a variety of taxa indicate that organisms with functional clocks consistently outcompete their clock-disrupted counterparts in rhythmic environments (37, 39, 137). It is currently unclear whether persistent circadian rhythms in some polar vertebrates relates only to synchronizing schedules with the geophysical environment, as interdependence between circadian clock function and homeostatic processes such as sleep and digestion have led some to hypothesize that rhythmicity may be adaptive even under constant conditions (97, 111, 129).

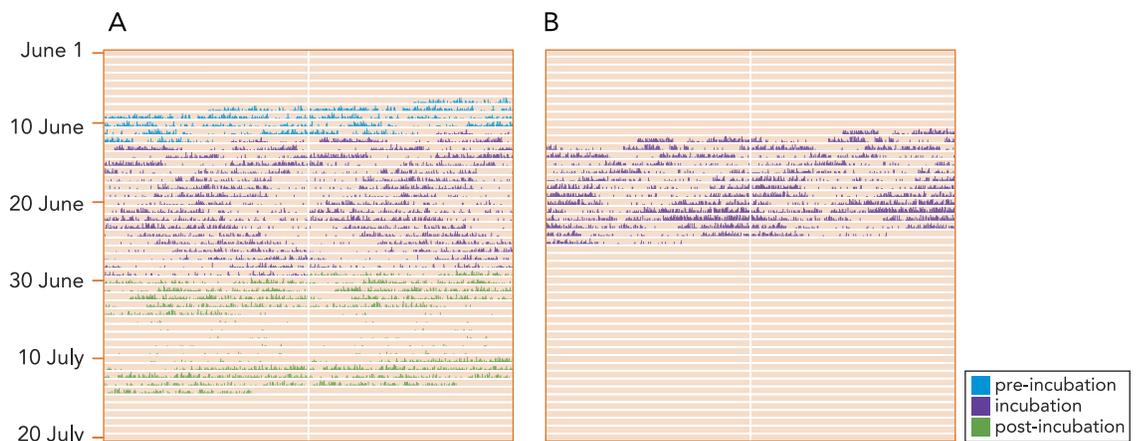
The physical environment in polar regions is neither constant nor arrhythmic; however, diel changes in ambient temperature, humidity, and light persist, with the amplitude of such rhythms

decreasing with increasing latitude. The persistence of entrained circadian rhythms of physiology and behavior in polar vertebrates may therefore function in synchronizing timing with these or other abiotic and ecological elements of the environment. The persistence of circadian rhythms in arctic ground squirrels, for example, is thought to be functional because it allows them to time their periods of above-ground activity to coincide with periods in the day when environmental conditions are more likely to be within their thermoneutral zone (72, 133, 135). Unlike some animals, ground squirrels are able to exploit a thermal refuge of a burrow system and nest, thereby avoiding exposure during the coldest time of day. In contrast, energetic savings of maintaining persistent rhythms may be absent or negligible for larger or nonburrowing animals at high latitudes.

For many polar vertebrates, the adaptive value of maintaining circadian rhythmicity may not be influenced directly by abiotic features of the environment but may instead relate to ecological interactions including diel variation in predation threat, prey or forage availability, and/or competition. Daan and Tinbergen (35), for example, reported a daily rhythm in the timing of young thick-billed murres (*Uria lomvia*) jumping from their breeding cliffs down to the sea. This behavioral rhythm allows murres to swamp their predators, although it is unclear whether the rhythm is driven by an entrained circadian oscillator or is a direct response to environmental cues (e.g., the change in light intensity). However, studies of circadian rhythms in polar vertebrates have principally taken

an organismal approach, and data on temporal dynamics within communities is generally lacking. Ecological effects on the persistence of circadian rhythms may be most obvious in the marine environment, where zooplankton DVM bring migrants from deep water into the epipelagic zone at night to feed and back at depth in daytime to avoid visual predators. These DVM affect the activity patterns of predators at higher trophic levels, including fish, marine mammals, and seabirds (55). Persistent zooplankton DVM at high latitudes has been reported at some locations during the polar day and polar night, although the strength and synchronicity of the DVM is weaker than in spring and fall (13, 14), and data on how rhythmicity in predators corresponds with zooplankton DVM at these sites is lacking. Other studies conducted during the polar day, however, have not detected the upward and downward movement of scattering layers that typically characterizes zooplankton DVM (17, 32). Cottier et al. (32) measured vertical migration of zooplankton in an arctic fjord at 79°N and found that individual zooplankton make unsynchronized migrations toward the surface each day, which may indicate migration is no longer under circadian control or circadian rhythms are no longer entrained to geophysical time.

Although circadian rhythms are typically entrained to the geophysical environment, free-running circadian rhythms can also be entrained by social cues (5, 80, 93), and this may be adaptive in some polar vertebrates. Steiger (116) found that, although semipalmated sandpipers (*Calidris pusilla*) express behavioral rhythms during incubation that



**FIGURE 3. Activity patterns of a male and a female semipalmated sandpiper** Activity patterns of a male (A) and a female (B) semipalmated sandpiper from a mated pair at 72°N displayed as a double-plotted actograms in which each row represents 2 consecutive days with bouts of activity (colored bars) interspersed with bouts of inactivity (white spaces). Time of day is indicated above the actogram, and color indicates breeding stage (red: pre-incubation; blue: incubation; green: post-incubation). Although individual semipalmated sandpipers do not maintain synchrony with geophysical time, both sexes display activity rhythms that are synchronized within the breeding pair, which allows them to coordinate incubation activities. These activity rhythms are <24 h and >24 h before and after the summer solstice, respectively. Although these rhythms are functional, they are not thought to be controlled by the circadian clock and may instead reflect an energy store-based interval timer with the switch in apparent tau reflecting changes in body composition or energy supply/demand. Pre- and post-incubation activity data are not available for the female. Figure adapted with permission from Ref. 116.

appear to free-run across the 24-h polar day, rhythms of individuals remain entrained to their partner such that mated pairs remain synchronized. Thus, although semipalmated sandpipers are not maintaining synchrony with the day, persistent circadian rhythms could allow them to coordinate incubation and chick-rearing activities within a mated pair (FIGURE 3). However, the behavioral rhythms detected in semipalmated sandpipers are not necessarily controlled by endogenous circadian clocks and may instead result from an energy store-based interval timer in which the incubating partner has to be relieved every 12 h or so. Lack of clock control is supported by the finding that artificially reducing the rate of egg cooling in semipalmated sandpiper nests by ~20% results in a 10% increase in mean incubation bout length (33).

Although the LD cycle is thought to be the primary driver for the emergence and evolution of endogenous clocks, a variety of physiological processes, including metabolic homeostasis, are now tightly linked to circadian regulation (11, 20), with dysregulation of circadian rhythms being associated with a variety of diseases (76, 94, 110). This has led to the hypothesis that circadian clocks may have additional “intrinsic” value, such that they maintain adaptive function, even in constant conditions (97, 111). The *Somalian cavefish Phreatichthys andruzzii*, for example, retains a functional food-entrainable molecular clock despite having evolved for millions of years in constant darkness, although the clock has developed an infradian period ( $\tau$  of ~47 h) and is no longer entrainable to light (27). Functionality of rhythms in polar vertebrates is typically discussed in the context of optimal timing of daily behaviors, with little consideration given to the intrinsic role circadian clocks play in coordinating metabolic functions. Furthermore, new questions emerge when the intrinsic functionality of clocks is considered with respect to how polar species that do not exhibit persistent rhythmicity avoid the metabolic pathologies typically associated with clock dysregulation.

## Humans in Polar Environments

The situation for biological rhythms of humans residing in polar regions is different from other polar vertebrates because humans are routinely exposed to artificial light, and timing of daily activities, including sleep-wake cycles, is governed by knowledge of clock-time and work/social schedules. Furthermore, most studies focus on people temporarily occupying these areas (e.g., bases in Antarctica); humans living in the arctic for generations (indigenous people) might be better able to cope with polar lighting conditions, although data supporting this hypothesis is lacking. Interestingly,

four human volunteers that overwintered in Antarctica (78°S) without knowledge of clock-time developed free-running circadian rhythms in their sleep/wake cycles, as well as in their excretion of melatonin, cortisol, and electrolytes (64). Two of the four individuals had unique free-running rhythms; the other two individuals were synchronized to one another. Similarly, free-running body temperature rhythms were observed in two volunteers who spent 18 days in July living at a remote hut in the arctic (79°N; Ref. 61).

For individuals overwintering in polar regions that do have knowledge of clock-time, disruptions of sleep-wake cycles, late sleep onset, and reductions in sleep efficiency, total sleep time, and slow-wave sleep are commonly reported, suggesting clock-function may be impaired (3, 16, 86). Additionally, some individuals suffer from seasonal affective disorder (SAD), a form of recurrent seasonal depression that is linked to disruption of circadian clock function (92). Although the etiology of SAD remains uncertain, disruption of brain monoamine transmission has been implicated (84, 99, 132). Recent studies indicate variation in the melanopsin gene (OPN4) is associated with the prevalence of SAD and with timing of sleep and activity (105, 106), supporting the hypothesis that these effects are associated with disruption of circadian rhythms. Although variance in the prevalence of SAD among immigrant groups has been reported at temperate latitudes (108, 122), some studies at higher latitudes have failed to detect seasonal changes in depression or sleep problems altogether (75, 114); the causes underlying discrepancies between studies are unclear. Altogether, it is apparent that humans are able to adjust to the polar day by behaviorally adjusting their exposure to light, although 24-h light can cause phase shifts (3). During the polar night, however, phase delays and clock disruption are more apparent and may have negative health consequences.

## Conclusions

Polar vertebrates exhibit diverse behavioral and physiological responses to the continuous lighting conditions during summers and winters at high latitudes, which may reflect variance in the ecological niches they occupy, as well as differences in their evolutionary histories. Our understanding of how light signals are captured and integrated by circadian systems has advanced markedly in the past decade, although it is currently unclear whether polar vertebrates have specific adaptations within their circadian photoreceptive pathways that increase sensitivity to subtle daily variation in the intensity or spectral quality of light. Functionality of persistent circadian rhythms in

polar vertebrates is generally thought to be linked to synchronization of physiology and behavior with the geophysical environment, although persistent rhythmicity may also be adaptive due to interdependence between circadian clock function and homeostatic processes. ■

This work was supported by grants from the National Science Foundation to C.L.B. (EF-0732763 and IOS-1147187), C.T.W. (IOS-1147187), and B.M.B. (EF-0732755 and IOS-1147232), as well as awards from the U.S. Army Medical Research and Materiel Command to B.M.B. (05178001). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

No conflicts of interest, financial or otherwise, are declared by the author(s).

Author contributions: C.T.W. drafted manuscript; B.M.B. and C.L.B. edited and revised manuscript; C.L.B. approved final version of manuscript.

References

1. Alerstam T, Gudmundsson GA, Green M, Hedenström A. Migration along orthodromic sun compass routes by arctic birds. *Science* 291: 300–303, 2001.
2. Andreasson S. Seasonal changes in diel activity of *Cottus poecilopus* and *C. gobio* (Pisces) at the Arctic Circle. *Oikos* 24: 16–23, 1973.
3. Arendt J. Biological rhythms during residence in polar regions. *Chronobiol Int* 29: 379–394, 2012.
4. Aschoff J. Exogenous and endogenous components in circadian rhythms. *Cold Spring Harb Symp Quant Biol* 25: 11–28, 1960.
5. Aschoff J, Fatranska M, Giedke H, Doerr P, Stamm D, Wisser H. Human circadian rhythms in continuous darkness: entrainment by social cues. *Science* 171: 213–215, 1971.
6. Aschoff J, Tokura H. Circadian activity rhythms in squirrel monkeys: entrainment by temperature cycles 1. *J Biol Rhythms* 1: 91–99, 1986.
7. Aschoff J, von Goetz C. Masking of circadian activity rhythms in canaries by light and dark. *J Biol Rhythms* 4: 29–38, 1989.
8. Ashley NT, Schwabl I, Goymann W, Buck CL. Keeping time under the midnight sun: behavioral and plasma melatonin profiles of free-living Lapland longspurs (*Calcarius lapponicus*) during the arctic summer. *J Exp Zool* 319: 10–22, 2013.
9. Ashley NT, Takayoshi U, Schwabl I, Goymann W, Salli BM, Bentley GE, Buck CL. Revealing a circadian clock in captive arctic-breeding songbirds, Lapland longspurs (*Calcarius lapponicus*), under constant illumination. *J Biol Rhythms*. In press.
10. Barrell GK, Montgomery GW. Absence of circadian patterns of secretion of melatonin or cortisol in Weddell seals under continuous natural daylight. *J Endocrinol* 122: 445–449, 1989.
11. Bass J, Takahashi JS. Circadian integration of metabolism and energetics. *Science* 330: 1349–1354, 2010.
12. Bellingham J, Chaurasia SS, Melyan Z, Liu C, Cameron MA, Tartzelin EE, Iuvone PM, Hankins MW, Tosini G, Lucas RJ. Evolution of melanopsin photoreceptors: discovery and characterization of a new melanopsin in nonmammalian vertebrates. *PLoS Biol* 4: e254, 2006.
13. Benoit D, Simard Y, Gagné J, Geoffroy M, Fortier L. From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. *Polar Biol* 33: 1505–1520, 2010.

14. Berge J, Cottier F, Last KS, Varpe Ø, Leu E, Søreide J, Eiane K, Falk-Petersen S, Willis K, Nygård H, Vogedes D, Griffiths C, Johnsen G, Lorentzen D, Brierley AS. Diel vertical migration of Arctic zooplankton during the polar night. *Biol Lett* 5: 69–72, 2009.
15. Berson DM. Strange vision: ganglion cells as circadian photoreceptors. *Trends Neurosci* 26: 314–320, 2003.
16. Bhattacharyya M, Pal MS, Sharma YK, Majumdar D. Changes in sleep patterns during prolonged stays in Antarctica. *Int J Biometeorol* 52: 869–879, 2008.
17. Blachowiak-Samolyk K, Kwasniewski S, Richardson K, Dmoch K, Hansen E, Hop H, Falk-Petersen S, Mouritsen LT. Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Mar Ecol Prog Ser* 308: 101–116, 2006.
18. Blanchong JA, McElhinny TL, Mahoney MM, Smale L. Nocturnal and diurnal rhythms in the unstriped Nile rat, *Arvicanthis niloticus*. *J Biol Rhythms* 14: 364–377, 1999.
19. Bloch G, Barnes BM, Gerkema MP, Helm B. Animal activity around-the-clock with no overt circadian rhythms: patterns, mechanisms and adaptive value. *Proc R Soc B* 280: 20130019, 2013.
20. Bray MS, Shaw CA, Moore MW, Garcia RA, Zanquetta MM, Durgan DJ, Jeong WJ, Tsai JY, Bugger H, Zhang D, Rohrwasser A, Rennison JH, Dyck JRB, Litwin SE, Hardin PE, Chow CW, Chandler MP, Abel ED, Young ME. Disruption of the circadian clock within the cardiomyocyte influences myocardial contractile function, metabolism, and gene expression. *Am J Physiol Heart Circ Physiol* 294: H1036–H1047, 2008.
21. Brown SA, Zumbunn G, Fleury-Olela F, Preitner N, Schibler U. Rhythms of mammalian body temperature can sustain peripheral circadian clocks. *Curr Biol* 12: 1574–1583, 2002.
22. Brown TM, Allen AE, al-Enezi J, Wynne J, Schlangen L, Hommes V, Lucas RJ. The melanopic sensitivity function accounts for melanopsin-driven responses in mice under diverse lighting conditions. *PLoS One* 8: e53583, 2013.
23. Buhr ED, Yoo SH, Takahashi JS. Temperature as a universal resetting cue for mammalian circadian oscillators. *Science* 330: 379–385, 2010.
24. Calhoun JB. Diel activity rhythms of the rodents, *Microtus ochrogaster* and *Sigmodon hispidus hispidus*. *Ecology* 26: 251–273, 1945.
25. Carlander KD, Cleary RE. The daily activity patterns of some freshwater fishes. *Am Midl Nat* 41: 447–452, 1949.
26. Cassone VM. Avian circadian organization: a chorus of clocks. *Front Neuroendocrinol* 35: 76–88, 2014.
27. Cavallari N, Frigato E, Vallone D, Fröhlich N, Lopez-Olmeda JF, Foà A, Berti R, Sánchez-Vázquez FJ, Bertolucci C, Foulkes NS. A blind circadian clock in cavefish reveals that opsins mediate peripheral clock photoreception. *PLoS Biol* 9: e1001142, 2011.
28. Challet E. Minireview: entrainment of the suprachiasmatic clockwork in diurnal and nocturnal mammals. *Endocrinology* 148: 5648–5655, 2007.
29. Chittka L, Stelzer RJ, Stanewsky R. Daily changes in ultraviolet light levels can synchronize the circadian clock of bumblebees (*Bombus terrestris*). *Chronobiol Int* 30: 434–442, 2013.
30. Cockrem JF. Plasma melatonin in the Adelle penguin (*Pygoscelis adeliae*) under continuous daylight in Antarctica. *J Pineal Res* 10: 2–8, 1991.
31. Cockrem JF. Circadian rhythms of plasma melatonin in the Adelle penguin (*Pygoscelis adeliae*) in constant dim light and artificial photoperiods. *J Pineal Res* 11: 63–69, 1991.
32. Cottier FR, Tarling GA, Wold A, Falk-Petersen S. Unsynchronized and synchronized vertical migration of zooplankton in a high arctic fjord. *Limnol Oceanogr* 51: 2586–2599, 2006.
33. Cresswell W, Holt S, Reid JM, Whitfield DP, Mellanby RJ. Do energetic demands constrain incubation scheduling in a biparental species? *Behav Ecol* 14: 97–102, 2003.
34. Cullen JM. The diurnal rhythm of birds in the arctic summer. *Ibis* 96: 31–46, 1954.
35. Daan S, Tinbergen J. Young guillemots (*Uria lomvia*) leaving their Arctic breeding cliffs: a daily rhythm in numbers and risk. *Ardea* 67: 96–100, 1979.

36. Damiola F, Le Minh N, Preitner N, Kornmann B, Fleury-Olela F, Schibler U. Restricted feeding uncouples circadian oscillators in peripheral tissues from the central pacemaker in the suprachiasmatic nucleus. *Genes Dev* 14: 2950–2961, 2000.
37. DeCoursey PJ, Walker JK, Smith SA. A circadian pacemaker in free-living chipmunks: essential for survival? *J Comp Physiol A* 186: 169–180, 2000.
38. Dibner C, Schibler U, Albrecht U. The mammalian circadian timing system: organization and coordination of central and peripheral clocks. *Annu Rev Physiol* 72: 517–549, 2010.
39. Dodd AN, Salathia N, Hall A, Kévei E, Tóth R, Nagy F, Hibberd JM, Millar AJ, Webb AA. Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. *Science* 309: 630–633, 2005.
40. Douglas RH, Jeffery G. The spectral transmission of ocular media suggests ultraviolet sensitivity is widespread among mammals. *Proc Roy Soc B* 281: 20132995, 2014.
41. Doyle S, Menaker M. Circadian photoreception in vertebrates. *Cold Spring Harb Symp Quant Biol* 72: 499–508, 2007.
42. Eloranta E, Timisjärvi J, Nieminen M, Ojutkangas V, Leppälouo J, Vakkuri O. Seasonal and daily patterns in melatonin secretion in female reindeer and their calves. *Endocrinology* 130: 1645–1652, 1992.
43. Enezi J, Revell V, Brown T, Wynne J, Schlangen L, Lucas R. A “melanopic” spectral efficiency function predicts the sensitivity of melanopsin photoreceptors to polychromatic lights. *J Biol Rhythms* 26: 314–323, 2011.
44. Falcón J, Besseau L, Sauzet S, Boeuf G. Melatonin effects on the hypothalamo-pituitary axis in fish. *Trends Endocrinol Metab* 18: 81–88, 2007.
45. Fernandes AM, Fero K, Driever W, Burgess HA. Enlightening the brain: Linking deep brain photoreception with behavior and physiology. *Bio Essays* 35: 775–779, 2013.
46. Folk GE. Observations on the daily rhythms of body temperature-labile mammals. *Ann NY Acad Sci* 98: 954–968, 1962.
47. Folk GE, Thrift DL, Zimmerman MB, Reimann PC. Mammalian activity-rest rhythms in Arctic continuous daylight. *Biol Rhythm Res* 37: 455–469, 2006.
48. Goldsmith R, Sladen W. Temperature regulation of some Antarctic penguins. *J Physiol* 157: 251–262, 1961.
49. Golombek DA, Rosenstein RE. Physiology of circadian entrainment. *Physiol Rev* 90: 1063–1102, 2010.
50. Griffiths DJ, Bryden MM, Kennaway DJ. A fluctuation in plasma melatonin level in the Weddell seal during constant natural light. *J Pineal Res* 3: 127–134, 1986.
51. Hankins MW, Peirson SN, Foster RG. Melanopsin: an exciting photopigment. *Trends Neurosci* 31: 27–36, 2008.
52. Harmer SL. The circadian system in higher plants. *Ann Rev Plant Biol* 60: 357–377, 2009.
53. Hattar S, Lucas RJ, Mrosovsky N, Thompson S, Douglas RH, Hankins MW, Lem J, Biel M, Hoffmann F, Foster RG, Yau KW. Melanopsin and rod-cone photoreceptive systems account for all major accessory visual functions in mice. *Nature* 424: 75–81, 2003.
54. Hau M, Romero LM, Brawn JD, Van't Hof TJ. Effect of polar day on plasma profiles of melatonin, testosterone, and estradiol in high-arctic Lapland longspurs. *Gen Comp Endocrinol* 126: 101–112, 2002.
55. Hays GC. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Migrations and Dispersal of Marine Organisms*. Dordrecht, The Netherlands: Springer, 2003, p. 163–170.
56. Hirayama J, Sassone-Corsi P. Structural and functional features of transcription factors controlling the circadian clock. *Curr Opin Genet Dev* 15: 548–556, 2005.
57. Hogg C, Neveu M, Stokkan KA, Folkow L, Cottrill P, Douglas R, Hunt DM, Jeffery G. Arctic reindeer extend their visual range into the ultraviolet. *J Exp Biol* 214: 2014–2019, 2011.
58. Hut RA, Scheper A, Daan S. Can the circadian system of a diurnal and a nocturnal rodent entrain to ultraviolet light? *J Comp Physiol A* 186: 707–715, 2000.
59. Hut RA, Pilonz V, Boerema AS, Strijkstra AM, Daan S. Working for food shifts nocturnal mouse activity into the day. *PLoS One* 6: e17527, 2011.
60. Johnson MS. Effect of continuous light on periodic spontaneous activity of white-footed mice (*Peromyscus*). *J Exp Zool* 82: 315–328, 1939.
61. Johnsson A, Engelmann W, Klemke W, Ekse AT. Free-running human circadian rhythms in Svalbard. *Zeitschrift für Naturforschung C Biosci* 34: 470–473, 1978.
62. Kalsbeek A, Kreier F, Fliers E, Sauerwein HP, Romijn JA, Buijs RM. Minireview: Circadian control of metabolism by the suprachiasmatic nuclei. *Endocrinology* 148: 5635–5639, 2007.
63. Karplus M. Bird activity in the continuous daylight of arctic summer. *Ecology* 33: 129–134, 1952.
64. Kennaway DJ, Van Dorp CF. Free-running rhythms of melatonin, cortisol, electrolytes, and sleep in humans in Antarctica. *Am J Physiol Regul Integr Comp Physiol* 260: R1137–R1144, 1991.
65. Kojima D, Mano H, Fukada Y. Vertebrate ancient-long opsin: a green-sensitive photoreceptive molecule present in zebrafish deep brain and retinal horizontal cells. *J Neurosci* 20: 2845–2851, 2000.
66. Kondo T, Strayer CA, Kulkarni RD, Taylor W, Ishiura M, Golden SS, Johnson CH. Circadian rhythms in prokaryotes: luciferase as a reporter of circadian gene expression in cyanobacteria. *Proc Natl Acad Sci USA* 90: 5672–5676, 1993.
67. Kroneld R. Phase shift of swimming activity in the burbot *Lota lota* L. (Pisces, Gadidae) at the Arctic Circle. *Physiol Zool* 49: 49–55, 1976.
68. Kronfeld-Schor N, Dayan T. Partitioning of time as an ecological resource. *Annual Rev Ecol Evol Syst* 153–181, 2003.
69. Krüml F. Zeitgeber for animals in the continuous daylight of high arctic summer. *Oecologia (Berl)* 24: 149–157, 1976.
70. Krüml F. The position of the sun is a possible zeitgeber for arctic animals. *Oecologia (Berl)* 24: 141–148, 1976.
71. Lei B, Yao G. Spectral attenuation of the mouse, rat, pig and human lenses from wavelengths 360 nm to 1020 nm. *Exp Eye Res* 83: 610–614, 2006.
72. Long RA, Martin TJ, Barnes BM. Body temperature and activity patterns in free-living arctic ground squirrels. *J Mamm* 86: 314–322, 2005.
73. Lu W, Meng QJ, Tyler NJ, Stokkan KA, Loudon AS. A circadian clock is not required in an arctic mammal. *Curr Biol* 20: 533–537, 2010.
74. Lucas RJ, Peirson SN, Berson DM, Brown TM, Cooper HM, Czeisler CA, Figueiro MG, Gamlin PD, Lockley SW, O'Hagan JB, Price LLA, Provencio I, Skene DJ, Brainard GC. Measuring and using light in the melanopsin age. *Trends Neurosci* 37: 1–9, 2014.
75. Magnusson A. An overview of epidemiological studies on seasonal affective disorder. *Acta Psychiatr Scand* 101: 176–184, 2000.
- 75a. Marshall AJ. Bird and animal activity in the arctic. *J Anim Ecol* 7: 248–250, 1938.
76. Martino TA, Oudit GY, Herzenberg AM, Nazneen T, Koletar MM, Kabir GM, Belsham DD, Backx PH, Ralph MR, Sole MJ. Circadian rhythm disorganization produces profound cardiovascular and renal disease in hamsters. *Am J Physiol Regul Integr Comp Physiol* 294: R1675–R1683, 2008.
77. Mayer WV. A preliminary study of the Barrow ground squirrel, *Citellus parryi barrowensis*. *J Mamm* 34: 334–345, 1953.
78. McMillan JP, Elliott JA, Menaker M. On the role of eyes and brain photoreceptors in the sparrow: arrhythmicity in constant light. *J Comp Physiol A* 102: 263–268, 1975.
79. Miché F, Vivien-Roels B, Pévet P, Spohner C, Robin JP, Le Maho Y. Daily pattern of melatonin secretion in an Antarctic bird, the emperor penguin, *Aptenodytes forsteri*: seasonal variations, effect of constant illumination and of administration of isoproterenol or propranolol. *Gen Comp Endocrin* 84: 249–263, 1991.
80. Mrosovsky N. Phase response curves for social entrainment. *J Comp Physiol A* 162: 35–46, 1988.
81. Müller K. Seasonal phase shift and the duration of activity time in the burbot, *Lota lota* (L.) (Pisces, Gadidae). *J Comp Physiol A* 84: 357–359, 1973.
82. Müller-Schwarze D. Circadian rhythms of activity in the Adélie penguin (*Pygoscelis adeliae*) during the austral summer. *Antarctic Res Ser* 12: 133–149, 1968.
83. Nakane Y, Ikegami K, Ono H, Yamamoto N, Yoshida S, Hirunagi K, Ebihara S, Kubo Y, Yoshimura T. A mammalian neural tissue opsin (Opsin 5) is a deep brain photoreceptor in birds. *Proc Natl Acad Sci USA* 107: 15264–15268, 2010.
84. Neumeister A, Willeit M, Praschak-Rieder N, Asenbaum S, Stastny J, Hilger E, Pirker W, Konstantinidis A, Kasper S. Dopamine transporter availability in symptomatic depressed patients with seasonal affective disorder and healthy controls. *Psychol Med* 31: 1467–1473, 2001.
85. Nilssen O, Lipton R, Brenn T, Hoyer G, Boiko E, Tkatchev A. Sleeping problems at 78 degrees north: the Svalbard Study. *Acta Psychiatr Scand* 95: 44–48, 1997.
86. Nordtug T, Melø TB. Diurnal variations in natural light conditions at summer time in arctic and subarctic areas in relation to light detection in insects. *Ecography* 11: 202–209, 1988.
87. Ohta H, Yamazaki S, McMahon DG. Constant light desynchronizes mammalian clock neurons. *Nat Neurosci* 8: 267–269, 2005.
88. O'Neill JS, Reddy AB. Circadian clocks in human red blood cells. *Nature* 469: 498–503, 2011.
89. Panda S, Sato TK, Castrucci AM, Rollag MD, DeGrip WJ, Hogenesch JB, Provencio I, Kay SA. Melanopsin (Opn4) requirement for normal light-induced circadian phase shifting. *Science* 298: 2213–2216, 2002.
90. Panda S, Provencio I, Tu DC, Pires SS, Rollag MD, Castrucci AM, Pletcher MT, Sato TK, Wiltsire T, Andahazy M, Kay SA, Van Gelder RN, Hogenesch JB. Melanopsin is required for non-image-forming photic responses in blind mice. *Science* 301: 525–527, 2003.
91. Park O, Roberts TW, Harris SJ. Preliminary analysis of activity of the cave crayfish, *Cambarus pellucidus*. *Am Nat* 75: 154–171, 1941.
92. Partonen T, Lönnqvist J. Seasonal affective disorder. *Lancet* 352: 1369–1374, 1998.

93. Paul MJ, Indic P, Schwartz WJ. Social forces can impact the circadian clocks of cohabiting hamsters. *Proc Roy Soc B* 281: 20132535, 2014.
94. Penev PD, Kolker DE, Zee PC, Turek FW. Chronic circadian desynchronization decreases the survival of animals with cardiomyopathic heart disease. *Am J Physiol Heart Circ Physiol* 275: H2334–H2337, 1998.
95. Pevet P, Challet E. Melatonin: both master clock output and internal time-giver in the circadian clocks network. *J Physiol* 105: 170–182, 2011.
96. Pickard Turek FW GE, Sollars PJ. Light intensity and splitting in the golden hamster. *Physiol Behav* 54: 1–5, 1993.
97. Pittendrigh CS. Temporal organization: reflections of a Darwinian clock-watcher. *Annu Rev Physiol* 55: 16–54, 1993.
98. Pohl H. 1999 Spectral composition of light as a zeitgeber for birds living in the high arctic summer. *Physiol Behav* 67: 327–337, 1999.
99. Praschak-Rieder N, Willeit M. Imaging of seasonal affective disorder and seasonality effects on serotonin and dopamine function in the human brain. *Curr Top Behav Neurosci* 11: 149–167, 2012.
100. Provencio I, Jiang G, Willem J, Hayes WP, Rollag MD. Melanopsin: An opsin in melanophores, brain, and eye. *Proc Natl Acad Sci USA* 95: 340–345, 1998.
101. Rea MS, Figueiro MG, Bierman A, Hamner R. Modeling the spectral sensitivity of the human circadian system. *Light Res Tech* 44: 386–396, 2011.
102. Refinetti R. Entrainment of circadian rhythm by ambient temperature cycles in mice. *J Biol Rhythms* 25: 247–256, 2010.
103. Reiherth E, Stokkan KA. Activity rhythm in high arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). *Can J Zool* 76: 2031–2039, 1998.
104. Reiherth E, Van't Hof TJ, Stokkan KA. Seasonal and daily variations in plasma melatonin in the high-arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). *J Biol Rhythms* 14: 314–319, 1999.
105. Roecklein KA, Rohan KJ, Duncan WC, Rollag MD, Rosenthal NE, Lipsky RH, Provencio I. A missense variant (P10L) of the melanopsin (*OPN4*) gene in seasonal affective disorder. *J Affect Disord* 114: 279–285, 2009.
106. Roecklein KA, Wong PM, Miller MA, Donofry SD, Kamarck ML, Brainard GC. Melanopsin, photosensitive ganglion cells, and seasonal affective disorder. *Neurosci Biobehav Rev* 37: 229–239, 2013.
107. Ruby NF, Brennan TJ, Xie X, Cao V, Franken P, Heller HC, O'Hara BF. Role of melanopsin in circadian responses to light. *Science* 298: 2211–2213, 2002.
108. Saheer TB, Lien L, Hauff E, Nirmal Kumar B. Ethnic differences in seasonal affective disorder and associated factors among five immigrant groups in Norway. *J Affect Disord* 151: 237–242, 2013.
109. Saini C, Morf J, Stratmann M, Gos P, Schibler U. Simulated body temperature rhythms reveal the phase-shifting behavior and plasticity of mammalian circadian oscillators. *Genes Develop* 26: 567–580, 2012.
110. Sephton S, Spiegel D. Circadian disruption in cancer: a neuroendocrine-immune pathway from stress to disease? *Brain Behav Immun* 17: 321–328, 2003.
111. Sharma VK. Adaptive significance of circadian clocks. *Chronobiol Int* 20: 901–919, 2003.
112. Silver R, LeSauter J, Tresco PA, Lehman MN. A diffusible coupling signal from the transplanted suprachiasmatic nucleus controlling circadian locomotor rhythms. *Nature* 382: 810–813, 1996.
113. Silverin B, Gwinner E, Van't Hof TJ, Schwabl I, Fusani L, Hau M, Helm B. Persistent diel melatonin rhythmicity during the Arctic summer in free-living willow warblers. *Horm Behav* 56: 163–168, 2009.
114. Sivertsen B, Øverland S, Krokstad S, Mykletun A. Seasonal variations in sleep problems at latitude 63°–65° in Norway. The Nord-Trøndelag Health Study, 1995–1997. *Am J Epidemiol* 174: 147–153, 2011.
115. Spurr EB. Diurnal activity of Adélie penguins *Pygoscelis adeliae* at Cape Bird. *Ibis* 120: 147–152, 1978.
116. Steiger SS, Valcu M, Spoelstra K, Helm B, Wikelski M, Kempenaers B. When the sun never sets: diverse activity rhythms under continuous daylight in free-living arctic-breeding birds. *Proc Roy Soc B* 280: 20131016, 2013.
117. Stelzer RJ, Chittka L. Bumblebee foraging rhythms under the midnight sun measured with radiofrequency identification. *BMC Biol* 8: 93, 2010.
118. Stokkan KA, Yamazaki S, Tei H, Sakaki Y, Menaker M. Entrainment of the circadian clock in the liver by feeding. *Science* 291: 490–493, 2001.
119. Stokkan KA, Van Oort BE, Tyler NJ, Loudon AS. Adaptations for life in the Arctic: evidence that melatonin rhythms in reindeer are not driven by a circadian oscillator but remain acutely sensitive to environmental photoperiod. *J Pineal Res* 43: 289–293, 2007.
120. Stokkan KA, Folkow L, Dukes J, Neveu M, Hogg C, Siefken S, Dakin SC, Jeffery G. Shifting mirrors: adaptive changes in retinal reflections to winter darkness in Arctic reindeer. *Proc Roy Soc B* 280: 20132451, 2013.
121. Strand JET, Aarseth JJ, Hanebrekke TL, Jørgensen EH. Keeping track of time under ice and snow in a sub-arctic lake: plasma melatonin rhythms in Arctic charr overwintering under natural conditions. *J Pineal Res* 44: 227–233, 2008.
122. Suhail K, Cochrane R. Seasonal changes in affective state in samples of Asian and white women. *Soc Psychiatry Psychiatr Epidemiol* 32: 149–157, 1997.
123. Swade RH, Pittendrigh CS. Circadian locomotor activity of rodents in the arctic. *Am Nat* 101: 433–466, 1967.
124. Tinbergen N. On the analysis of social organization among vertebrates, with special reference to birds. *Am Midl Nat* 21: 210–234, 1939.
125. Tomotani BM, Flores DE, Tachinardi P, Paliza JD, Oda GA, Valentinuzzi VS. Field and laboratory studies provide insights into the meaning of daytime activity in a subterranean rodent (*Ctenomys aff. knighti*), the tuco-tuco. *PLoS One* 7: e37918, 2012.
126. van der Vinne V, Riede SJ, Gorter JA, Eijer WG, Sellix MT, Menaker M, Daan S, Pilonz V, Hut RA. Cold and hunger induce diurnality in a nocturnal mammal. *Proc Natl Acad Sci USA* 111: 15256–15260, 2014.
127. van Oort BEH, Tyler NJC, Gerkema MP, Folkow Blix AS, Stokkan KA. Circadian organization in reindeer. *Nature* 438: 1095–1096, 2005.
128. van Oort BEH, Tyler NJC, Gerkema MP, Folkow L, Stokkan KA. Where clocks are redundant: weak circadian mechanisms in reindeer living under polar photic conditions. *Naturwissenschaften* 94: 183–194, 2007.
129. Vaze KM, Sharma VK. On the adaptive significance of circadian clocks for their owners. *Chronobiol Int* 30: 413–433, 2013.
130. Welsh JH. Diurnal rhythms. *Q Rev Biol* 13: 123–139, 1938.
131. Westin L, Aneer G. Locomotor activity patterns of nineteen fish and five crustacean species from the Baltic Sea. *Envir Biol Fishes* 20: 49–65, 1987.
132. Willeit M, Praschak-Rieder N, Neumeister A, Pirker W, Asenbaum S, Vitouch O, Tauschera J, Hilgera E, Stastnya J, Brücke T, Kasper S. [<sup>123</sup>I]-β-CIT SPECT imaging shows reduced brain serotonin transporter availability in drug-free depressed patients with seasonal affective disorder. *Biol Psychiatry* 47: 482–489, 2000.
133. Williams CT, Barnes BM, Buck CL. Body temperature rhythms persist under the midnight sun but are absent during hibernation in free-living arctic ground squirrels. *Biol Lett* 8: 31–3, 2012.
134. Williams CT, Barnes BM, Richter MR, Buck CL. Hibernation and circadian rhythms of body temperature in free-living arctic ground squirrels. *Physiol Biochem Zool* 85: 397–404, 2012.
135. Williams CT, Wilsterman K, Kelley AD, Breton AR, Stark H, Humphries MM, McAdam AG, Barnes BM, Boutin S, Buck CL. Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semi-fossorial rodents. *J Mamm*. In press.
136. Wilson RP, Culik B, Coria NR, Adelung D, Spairani HJ. Foraging rhythms in Adélie penguins (*Pygoscelis adeliae*) at Hope Bay, Antarctica; determination and control. *Polar Biol* 10: 161–165, 1989.
137. Woelfle MA, Ouyang Y, Phanvijhitsiri K, Johnson CH. The adaptive value of circadian clocks: an experimental assessment in cyanobacteria. *Curr Biol* 14: 1481–1486, 2004.
138. Yamada H, Oshima I, Sato K, Ebihara S. Loss of the circadian rhythms of locomotor activity, food intake, and plasma melatonin concentration induced by constant bright light in the pigeon (*Columba livia*). *J Comp Physiol A* 163: 459–463, 1988.
139. Yammouni R, Bozzano A, Douglas RH. A latitudinal cline in the efficacy of endogenous signals: evidence derived from retinal cone contraction in fish. *J Exp Biol* 214: 501–508, 2011.
140. Yerushalmi S, Green RM. Evidence for the adaptive significance of circadian rhythms. *Ecol Lett* 12: 970–981, 2009.