

Evolution of Animal Photoperiodism

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Key Words

circannual rhythm, climatic adaptation, dormancy, migration, seasonality

Abstract

Photoperiodism is the ability of organisms to assess and use the day length as an anticipatory cue to time seasonal events in their life histories. Photoperiodism is especially important in initiating physiological and developmental processes that are typically irrevocable and that culminate at a future time or at a distant place; the further away in space or time, the more likely a seasonal event is initiated by photoperiod. The pervasiveness of photoperiodism across broad taxa, from rotifers to rodents, and the predictable changes of photoperiodic response with geography identify it as a central component of fitness in temperate and polar seasonal environments. Consequently, the role of day length cannot be disregarded when evaluating the mechanisms underlying life-historical events, range expansions, invasions of novel species, and response to climate change among animals in the temperate and polar regions of the world.

Of the four seasons, none lasts forever; of the days some are long and some are short.

Sun Tzu 6:31

INTRODUCTION

In seasonal environments, no life cycle can be complete without the means to exploit the favorable season, to avoid or mitigate the unfavorable season, and to switch between the two lifestyles in a timely manner. Animals exploit the favorable season through growth, development, and reproduction; many animals avoid or mitigate the unfavorable season through dormancy and migration. Successful individuals must be prepared for the appropriate seasonal activities when that season arrives. Reproducing too late in the fall exposes individuals to the exigencies of winter; entering dormancy too early misses the opportunity for continued reproduction and reduces nutritional reserves accumulated for overwintering and for reproduction the following spring. Fitness for animals in a seasonal environment then involves not only the abilities to cope with the changing seasons, but also the ability to express the appropriate phenotype so as not to miss out on opportunities and, at the same time, not to be exposed to lethal conditions. Fitness in seasonal environments is all about timing: the optimal time to migrate and reproduce, the optimal time to stop reproducing, and the optimal time to migrate again. Each of these activities requires preparation: acquiring resources or territories for reproduction, building up fat stores for dormancy, or molting old for new feathers for migration. For most animals, these go/no-go seasonal decisions are irrevocable, either for the lifetime of the individual or within the context of the normal progression of the seasons. Hence, fitness is dependent not only upon the optimal time for engaging in season-specific activities, but also upon the ability to forecast and prepare for the changing seasons in advance of their arrival.

A wide variety of animals from diverse taxa uses the day length or photoperiod as an anticipatory cue to make seasonal preparations. Photoperiod is most useful in predicting environmental conditions in the future or at distant localities; photoperiod provides a go/no-go signal that initiates a usually irrevocable cascade of physiological and developmental processes that culminate in reproduction, dormancy, or migration. Photoperiod, in addition to food, temperature, and other factors in the immediate environment, then affects the rates at which these processes proceed.

Experimental evaluation of photoperiodic response is more cumbersome than evaluating responses to other variables, most notably temperature; however, a correct photoperiodic response is a more important component of fitness than temperature in temperate and polar environments, where the predictability of seasonal change and its strong correlation with day length enable animals to exploit favorable temperatures and to avoid or mitigate unfavorable temperatures.

In this review, we show that photoperiodism is widespread among animals and that its evolution among taxa reveals many consistencies and some inconsistencies yet to be resolved. Most importantly, we show that photoperiodism cannot be disregarded when evaluating the mechanisms underlying life-historical events in any animal living at temperate and polar latitudes. Although we have made a comprehensive study of the literature on photoperiodism in all major animal taxa, the role of day length is well understood in only a few of those groups. We, however, review all taxa in which

credible studies have been undertaken, emphasize case studies that illustrate general principles, comment on commonalities and differences of photoperiodism among taxa, discuss implications for rapid climate change, and propose avenues for future research on the evolution of photoperiodism.

DAY LENGTH, SEASONALITY, AND PHOTOPERIODIC RESPONSE

Why Use Day Length?

Timing is crucial for maximal exploitation of the favorable season and for minimal exposure to the unfavorable season. However, reproduction, migration, and dormancy require physiological and developmental preparations that must be made in advance of the actual seasonal event. Day length provides a highly reliable calendar that animals can use to anticipate and prepare for seasonal change. Unlike temperature and rainfall, day length at a given spot on Earth is the same today as it was on this date 10 or 10,000 years ago. Hence, day length provides a consistent predictor of future environmental conditions over evolutionary time, enabling animals to use day length to prepare for and to optimize the timing of reproduction, dormancy, and migration in their seasonal life histories. Importantly, both seasonality and day length vary with changing geography.

Geographic Variation in Seasonality, Day Length, and Photoperiodism

The seasonal environment determines the optimal time to reproduce, migrate, or go dormant. In a population of individuals, each with its own genetically determined response to day length, some individuals will reproduce, migrate, or go dormant at the optimal time and thereby achieve greater fitness than others that reproduce, migrate, or go dormant at earlier or later times (Bradshaw et al. 2004, Cooke 1977, Lambrechts et al. 1997, Quinn et al. 2000, Templeton 1986). Hence, the seasonal environment imposes optimizing (stabilizing) selection within a population on the day length individuals use to time events in their seasonal life histories. Below, we describe how seasonality (the selective force) and day length (the environmental cue) change with geography, and then how photoperiodism (the biotic response) is integrated into geographically variable seasonal and photic contexts.

How does seasonality change with geography? Because of the 23° tilt of Earth's axis of daily rotation relative to the plane of its annual rotation about the Sun, the Northern and Southern Hemispheres experience opposite periods of summer and winter. Also because of this tilt, not only is winter day length shorter at higher than at lower latitudes, but also the angle of incident winter sunlight is more acute and imparts less heat per hour of daylight. Consequently, the latitudinal gradient in climate is primarily one of winter cold rather than summer heat (**Figure 1a**) and, as one proceeds poleward, spring arrives later and fall arrives earlier. Hence, the length of the favorable season declines regularly with increasing latitude. For example, in **Figure 1a**, the

period: the time required for a rhythm to complete one full cycle, or time from peak to peak of a rhythm

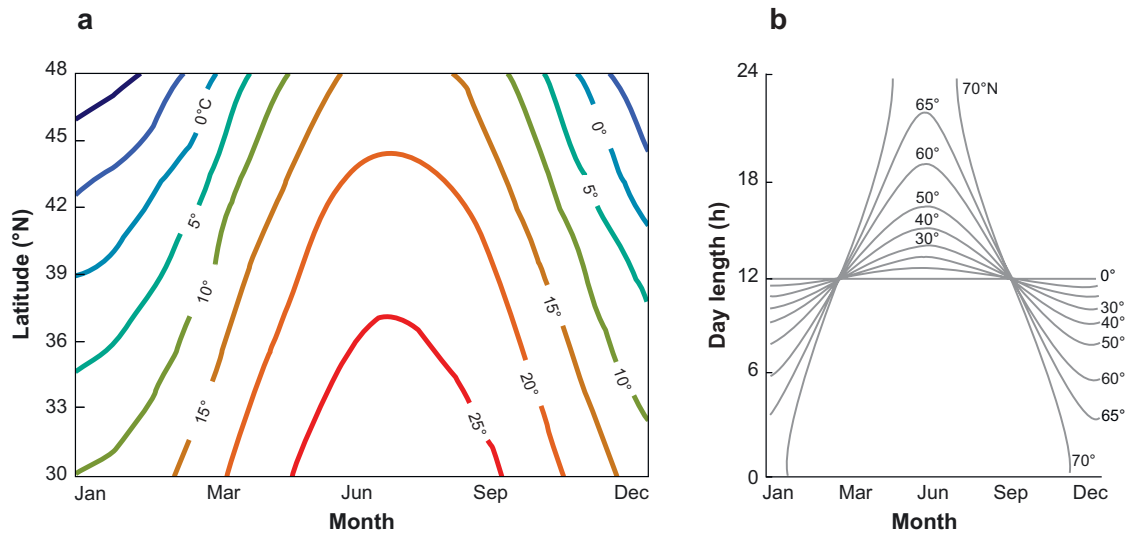


Figure 1

Geographic and seasonal variation in temperature and day length. (a) Isotherms for mean monthly temperature in central and eastern North America (Bradshaw et al. 2004). The latitudinal variation in climate is less a matter of summer warmth (June isotherms are far apart) than winter cold (January isotherms are close together), and northern populations experience a shorter growing season than southern populations. Hence, changes in season length and the timing of spring and fall activities have a greater effect on animal populations than do the direct effects of temperature. (b) Seasonal patterns in day length (sunrise to sunset) at different latitudes ($^{\circ}\text{N}$) in the Northern Hemisphere (Danilevskii 1965). Day length at temperate and polar latitudes predicts future seasons more reliably than any other environmental cue.

15°C isotherm declines from 10.5 months at 30°N to 3 months at 48°N . When air masses encounter mountain ranges, they rise, expand, and cool so that the length of the favorable season also declines with increasing altitude (MacArthur 1972). In eastern North America, the number of freeze-free days decreases by approximately 9.3 days with every degree of increasing latitude, and by 94 days with every 1000 m of increasing elevation (Bradshaw 1976). Seasonal activities of temperate animals are therefore intimately related to the coming of spring and fall and to the length of the growing season. As the length of the growing season and the coming of spring and fall vary with geography, so do the optimal times to initiate growth, development, reproduction, dormancy, or migration.

How does day length vary with geography? Also because of Earth's tilt, day length varies with both time of year and latitude (**Figure 1b**). At the equator, Earth's surface receives 12 hours of light per day (sunrise to sunset) all year long. As one proceeds north or south of the equator, the annual variation in day length becomes progressively more extreme, increasing from 0 h at the equator to 24 h in the summer at latitudes greater than 67° . There are several consequences of these patterns for animals using

photoperiod to time their seasonal activities. First, at tropical latitudes below approximately 15°, the annual change in day length is not sufficient to provide a reliable seasonal cue. Even so, a few insects are responsive to day lengths at latitudes as low as 7°–9° (Norris 1965, Wolda & Denlinger 1984). Second, above 30° latitude, wherein lies the greatest proportion of Earth's landmass, day length provides a strong and highly reliable seasonal cue over evolutionary time. Third, at very high latitudes, animals encounter near-constant light in the summer and near-constant darkness during the winter. Consequently, animals must have mechanisms to cope with constant day length experienced by migratory animals in the tropics, rapidly changing day lengths encountered during spring and fall migrations, constant light at high latitudes, and constant darkness during the winter at high latitudes or subterranean hibernacula.

How does photoperiodism integrate with seasonal and geographic variation in day length?

So far in this discussion, we have treated absolute day length as the cue that times seasonal activities. This description is valid for the initiation of dormancy (diapause) in most arthropods and many short-lived vertebrates; for most deuterostomes, the timing of seasonal events represents an interaction between day length, circannual rhythmicity, and refractoriness. Circannual rhythms are endogenous (internal, self-sustained) physiological rhythms that persist under constant photoperiod and temperature. The period of this rhythm usually varies from 9–15 months and the rhythm can persist for several to as many as 10 years (Dawson 2002, Gwinner 1996). Under natural conditions, the circannual clock is set by seasonally changing day lengths. Short days in the late summer will lead to corrective advances of the rhythm because the circannual clock will be perceived as running behind real time; short days in the early summer will lead to corrective delays of the rhythm because the circannual clock will be perceived as running ahead of real time (Bromage et al. 2001). Finally, at specific times in their life cycles, animals may become refractory (nonresponsive) to day length. After reproduction, many birds and mammals become refractory to long days, thereby enabling them to ignore otherwise favorable conditions and to prepare for migration or dormancy in a timely manner. Responsiveness to long days is then usually restored by experiencing short days (Dawson 2002, Goldman et al. 2004). Most arthropods use day length to initiate dormancy (diapause), but, upon entering the diapause state, become refractory to photoperiod. Diapause is then terminated spontaneously or in response to prolonged cold temperatures (chilling) (Danks 1987, Tauber et al. 1986).

The interaction of photoperiodic, circannual rhythmicity and refractoriness not only enhances the ability of animals to time their seasonal development at intermediate latitudes, but also enables them to keep track of seasonal time with either unchanging or rapidly changing day lengths.

Does having the proper photoperiodic response actually affect fitness? Typical reciprocal transplant experiments cannot answer this question. Because of the covariation between the annual change in day length and seasonality (**Figure 1**), photoperiodic adaptation and seasonal adaptation will always be confounded in nature. Questions of potential effects of climate warming can be correctly assessed by

circannual: an internal, self-sustained rhythm with a period of approximately one year

refractoriness: nonresponsiveness to day length; may be spontaneous or induced by day length itself

circadian: an internal, self-sustained rhythm with a period of approximately one day

amplitude: one-half of the maximum and minimum expression of a rhythm, or one-half the difference between a peak and a valley in a rhythm

transplants up and down a mountain or across longitudes at the same latitude. Transplants can also test for simple, local adaptations by asking if individuals of a species are more fit in one locality or another, but only so long as causality is not inferred. Our solution to this conundrum was to perform reciprocal transplants of the mosquito *Wyeomyia smithii* in controlled-environment rooms where we could program actual annual changes in day length while holding seasonality constant (Bradshaw et al. 2004). We measured fitness of southern, midlatitude, and northern populations (from 30°N–50°N) as the year-long cohort replacement rate, integrating the effects of all four seasons in a thermally benign midlatitude seasonal year. We either enforced the optimal seasonal timing of diapause and development with unambiguous long and short days (control) or programmed the natural midlatitude photoperiod. Relative to the control, southern populations entered diapause too late and lost 74% of fitness; northern populations entered diapause too early and lost 88% of fitness. The midlatitude populations suffered no loss in fitness. Hence, fitness was critically dependent on possessing the genetically determined correct response to day length. We know of no other study that has determined a composite index of fitness in a realistic seasonal setting where the annual change in day length has been varied while holding seasonality constant.

DOES PHOTOPERIODISM COEVOLVE WITH CIRCADIAN RHYTHMICITY?

In 1936, Bünning (1936) proposed that circadian rhythms regulating daily activities formed the basis (*Grundlage*) of the photoperiodic timer regulating seasonal activities. Bünning's hypothesis has had enduring appeal because, if true, it would mean that a single mechanism is responsible for the regulation of both daily and seasonal cycles in animals. If, however, the same suite of genes responsible for the expression of seasonal timing is also responsible for the expression of daily cycles, then adaptive modification of photoperiodic time measurement necessarily implies genetic modification of the circadian clock, that is, the two must evolve together because of the causal, pleiotropic relationship between them. If genetic variation in photoperiodic response were caused by genetic variation in the circadian clock, then there should be a correlation between photoperiodic responsiveness and genetically determined variation in (*a*) the period or amplitude of circadian clock expression, (*b*) the time of the onset of circadian activity each day, or (*c*) the duration of circadian activity each day (Majoy & Heideman 2000). We acknowledge that we do not cover the many studies on the relationship between circadian rhythms and photoperiodism conducted on single, often highly inbred, long-established lab stocks that have experienced only daily and not seasonal cycles for many generations. Rather, we focus on studies that have considered covariation of photoperiodism (the trait under selection) and circadian rhythmicity (the putative causal mechanism) over evolutionary time across a geographic gradient of seasonality (the selective force).

First, in the white-footed mouse, *Peromyscus leucopus*, southern populations are nonresponsive to short days and reproduce year round; northern populations are polymorphic in response to short days so that some mice undergo reproductive regression

in the winter, whereas other mice in the same population may continue to reproduce throughout the year (Heideman et al. 1999, Lynch et al. 1981). Northern and southern populations do not differ in the period of the circadian activity rhythm in constant darkness or in the timing or duration of nocturnal activity under either long or short days (Carlson et al. 1989). Similar responses are obtained in comparison of lines from within a single population divergently selected for response and nonresponse to short days (Majoy & Heideman 2000). Within a single northern population, circadian entrainment maintained a stable pattern for 30 weeks through gonadal regression and spontaneous redevelopment, and mice did not differ in the timing of activity onset after lights off (Johnston & Zucker 1980). These results indicate that in *P. leucopus*, neither genetic variation within populations nor the genetic differences between populations in photoperiodic response is due to a corresponding genetic modification in formal properties of the circadian clock. Rather, genetic variation in *P. leucopus* and its congener, *P. maniculatus*, is due to the effects of melatonin on target organs downstream from the circadian clock (Desjardins et al. 1986, Heath & Lynch 1982, Ruf et al. 1997).

Second, in the pitcher-plant mosquito *W. smithii*, the switching day length (critical photoperiod) regulating larval diapause increases regularly with latitude and altitude ($R^2 > 0.90$ repeatedly) and the critical photoperiod varies by 10 SD of mean phenotype from 30°N–50°N (Bradshaw & Holzapfel 2001a,b). However, neither the period nor the amplitude of the circadian rhythm is correlated with critical photoperiod over the same geographic range (Bradshaw et al. 2003, 2006). These results indicate that photoperiodic response and circadian rhythmicity have evolved independently of each other over the climatic gradient of eastern North America.

Third, in *Drosophila littoralis*, critical photoperiod is correlated with both the median timing of adult eclosion and the free-running eclosion rhythm over 30° latitude in Eastern Europe (Lankinen 1986). However, this covariation of photoperiodism with the eclosion rhythm is due to linkage and not pleiotropy, that is, closely linked but different genes (Lankinen & Forsman 2006).

These results do not mean that no circadian genes are involved in photoperiodism, incidental to their functional role in the circadian clock. Given the pervasiveness of circadian rhythmicity on cellular physiology in general (Claridge-Chang et al. 2001, McDonald & Rosbash 2001), we would be surprised if circadian rhythmicity had zero effect on the expression of photoperiodic response. In Syrian (golden) hamsters, a mutation in the circadian rhythm gene *casein kinase 1ε (tau)* changes both the period of the circadian wheel-running rhythm (Ralph & Menaker 1988) and the total period (light + dark) under which hamsters are photoperiodic (Shimomura et al. 1997). In various flies (Diptera), there is increasing evidence that the circadian rhythm gene *timeless* somehow affects photoperiodic control of diapause (Goto et al. 2006; Mathias et al. 2005, 2007; Pavelka et al. 2003). The noninvolvement of circadian rhythmicity in the evolution of photoperiodism in mice, mosquitoes, and flies does, however, mean that whatever the connection between the circadian clock and the photoperiodic timer within specific populations, this connection does not impede their independent evolution in nature. In sum, comparisons between photoperiodic time measurement and circadian expression across climatic gradients in mice, mosquitoes, and flies indicate

entrainment: ability of a zeitgeber to regulate or drive the period of an otherwise self-sustained rhythm

critical photoperiod: day length stimulating 50% development and 50% dormancy, or the day length at the inflection point of a photoperiodic response curve

that the photoperiodic timer and the circadian clock are capable of and, indeed, have undergone independent evolution over seasonal climatic gradients in both North America and Europe.

PREVALENCE OF PHOTOPERIODISM AMONG ANIMALS

Photoperiodism has been documented in rotifers, annelids, mollusks, arthropods, echinoderms, bony fish, frogs, turtles, lizards, birds, and mammals. In general, photoperiod provides the go/no-go cue for the direct timing of seasonal events, or for the initiation of physiological, endocrinological, and developmental cascades that, once started, are irrevocable or, at least under natural conditions, usually not reversed before the completion of the seasonal event under selection. In ectotherms, photoperiod can interact with temperature to modulate rates of conversion to sexual forms in an oligochaete annelid (Schierwater & Hauenschild 1990), rates of egg laying in a freshwater snail (Joose 1984), rates of vernal development in tree-hole mosquitoes (Holzapfel & Bradshaw 1981), rates of smoltification in Atlantic salmon (McCormick et al. 1998), accelerated feeding in frogs (Wright et al. 1988), thermal preferences in turtles (Graham & Hutchison 1979, Hutchison & Maness 1979, Kosh & Hutchison 1968), and temperature-dependent rates of metabolism (Angilletta 2001), growth rate (Uller & Olsson 2003), and thermal homeostasis (Lashbrook & Livezey 1970) in lizards.

Photoperiod by itself is crucial for the go/no-go initiation of events that occur at future times or distant places. The optimal timing of these long-range transitions is determined by selection over many years. Interaction of photoperiod with temperature in ectotherms then fine-tunes the actual completion of those events in concert with annual variation in the thermal environment.

Invertebrates

Other than arthropods, the literature on photoperiodism in most invertebrate groups, including invertebrate chordates, is scant. Nonetheless, we did find examples of photoperiodism in rotifers, annelids, mollusks, and echinoderms.

Rotifers. In the monogonont rotifer *Notommata copeus*, long days provide the go/no-go signal for switching from parthenogenetic to mictic females. Mictic females lay haploid eggs that develop into either males or haploid females that, when fertilized, produce diapausing female embryos (Pourriot & Clément 1975).

Annelids. In polychaetes, increasing day lengths initiate the seasonal reproductive cycle of *Nereis (Neanthes) limnicola* (Fong & Pease 1992). Photoperiodic setting of the circannual clock in the semelparous *N. virens* determines the irrevocable switch from somatic to reproductive growth (Last & Olive 1999, 2004). In the oligochaete *Sylvaria lacustris*, short days stimulate the irreversible switch from vegetative to sexual reproduction and formation of overwintering cocoons (Schierwater & Hauenschild 1990).

Mollusks. We could not find any clear studies of photoperiodism in bivalves, cephalopods, chitins, or marine gastropods. In the freshwater snail *Lymnaea stagnalis*, long days control the rate of egg laying and override inhibitory effects of both low temperature and starvation (Joose 1984). In the terrestrial snail *Helix aspersa*, short days trigger both dormancy and supercooling ability (Ansart et al. 2001), and in the terrestrial slug *Limax valentianus*, photoperiod is the essential factor regulating both the initiation of reproduction and the rate of egg production (Hommay et al. 2001).

Arthropods. The literature on arthropod photoperiodism is vast. Generalizations about the use of photoperiodism in insects are highly elusive and, indeed, “it is fair to say that for every life cycle that we consider potentially reasonable controlled by external cues, some insect can be found to illustrate it” (Danks 1994, p. 357). Several excellent and comprehensive reviews exist on photoperiodic and physiological control of seasonal development in arthropods (Danilevskii 1965, Danks 1987, Saunders 2002, Tauber et al. 1986, Nijhout 1994). From this literature, we make several generalizations about photoperiodism in arthropods.

1. Photoperiod provides the primary go/no-go signal for the initiation of neuroendocrine cascades leading to diapause, migration, or reproduction. Photoperiod may also modulate the rates of completion of these events through its interaction with food, temperature, and moisture. When there is an interaction between photoperiod and temperature, high temperatures tend to reinforce long-day effects, and low temperatures short-day effects.
2. The switching day length (critical photoperiod) initiating diapause increases regularly with latitude and altitude, where the correlation between critical photoperiod and geography can exceed 0.95. To our knowledge, this generalization is the most robust of any ecogeographic rule.
3. The critical photoperiod usually occurs approximately a generation before the onset of adverse conditions. Indeed, the importance of photoperiod as a long-term, reliable, and predictive cue lies in its ability to induce diapause at the optimal time of year, even when temperature and food are otherwise favorable for growth, development, and reproduction.
4. In temperate environments with warm, moist summers and harsh winters, especially in midcontinental or eastern continental climates, long-day arthropods usually enter a hibernal diapause that is initiated by short or shortening days. In temperate environments with hot, dry summers and mild winters, especially on western continental slopes, short-day arthropods may enter an aestival diapause that is initiated by long days or enter both an aestival and hibernal diapause cued by opposite day lengths.
5. High-latitude or polar arthropods may extend development over two or more years, and individuals may enter a photoperiodically mediated diapause two or more times at two or more stages during their life cycles.
6. Photoperiodic response is a polygenic trait, generally with a high heritability and a complex underlying genetic architecture involving pleiotropy, dominance, and epistasis.

7. Photoperiod is generally important for timing the switch from continuous development to diapause, but diapause is usually terminated spontaneously or in response to prolonged exposure to cold temperatures (chilling).
8. Among arthropods, photoreception related to photoperiodism may involve the ocelli, the compound eyes, or the brain itself. After interpretation of day length, the go/no-go photoperiodic response is initiated from the brain via peptide hormones to the corpora allata (allatostatins and allatoropins) that regulate the release of juvenile hormone (a terpenoid), or to the prothoracic glands (prothoracicotropic hormone) that release ecdysteroid, or, in *Bombyx mori*, via neural connections to the subesophageal ganglion that releases diapause hormone (a peptide). For most arthropods, photoperiodic control of seasonal polyphenisms and seasonal development, diapause, migration, and reproduction involves juvenile hormone, ecdysteroid, or their interaction.

Echinoderms. Gametogenesis in the sea urchin *Strongylocentrotus purpuratus* requires the shortening day lengths of fall and short days of winter; gametogenesis in the starfish *Pisaster ocraceus* depends upon the increasing day lengths of spring and long days of summer. In both species, the principal roles of photoperiod are in the initiation of physiological and developmental processes that ultimately culminate in reproduction and in the setting of the circannual clock that mediates seasonal windows for the timing of reproduction. In *P. ocraceus*, the effect of day length on gonadogenesis remains intact after removal of the terminal eyespots (ocelli), indicating that the terminal ocelli are not necessary for the go/no-go timing of seasonal reproduction (Halberg et al. 1987, Pearse et al. 1986).

Cephalochordates, Jawless Craniata, and Cartilaginous Fishes

We found no evidence for photoperiodic regulation of seasonal growth, development, or reproduction in amphioxus, hagfish, lampreys, or dogfish. The critical experiments for detecting photoperiodically timed life-history events have either not been run (amphioxus, hagfish, skates, or rays) or have considered only one life-cycle transition: metamorphosis in the sea lamprey *Pteromyzon marinus* (Holmes et al. 1994) or embryogenesis in the dogfish *Scyliorhinus canicula* (Thomason et al. 1996). We know of no studies that have examined the effect of day length on gonadal development, sexual maturation, or reproduction in any of these groups. The apparent presence of photoperiodism and circannual rhythms in echinoderms indicates that photoperiodism and its regulation of circannual rhythmicity either appeared early in deuterostome evolution and were lost (or were not looked for) in cephalochordates, hagfish, lampreys, and cartilaginous fish, or evolved separately in echinoderms and bony vertebrates, where photoperiod provides pivotal go/no-go signals for the seasonal timing of life-history events in teleost fish and tetrapods.

Bony Vertebrates

Photoreception. Vertebrate life cycles in general consist of a reproductive stage brought on by a combination of direct effects of absolute day length, increasing

day lengths, entrainment (setting) of the circannual clock by photoperiod, and temperature. Usually, day length and the circannual clock are the most important for providing the go/no-go signal that initiates seasonal gonadal development or migration, and more proximal environmental factors such as temperature and food affect mating and the actual production of offspring. The reproductive condition may become refractory (nonresponsive) to long days either spontaneously or in response to long summer days. Refractoriness is generally terminated by short days, declining day lengths, cold temperatures (commonly in ectotherms), or a combination of these factors. The refractory period provides nonreproductive time to accumulate nutritional reserves before winter or to molt before migration, when days are warm and resources abundant.

Among vertebrates, photoreception related to photoperiodism is exclusively retinal in mammals and may involve retinal, pineal, or deep brain (mediobasal hypothalamus) photoreceptors in other vertebrates (Björnsson 1997, Borg et al. 2004, Bromage et al. 2001, Dawson et al. 2001, Dawson 2002, Tosini 1997, Tosini et al. 2001, Vigh et al. 2002). There are two general hypotheses concerning the adaptive significance of possessing extraretinal photoreception for biological timing. First, vision requires focused representation of the environment, and a point on the retina projects to a precise positional map in the brain. By contrast, an irradiance detector integrates light from the whole field of view, as would occur from pineal or deep-brain photoreception (Foster et al. 1994). Even in mammals where light enters via the retina, photoreception is mainly by the retinal ganglion cells (Menaker 2003), and neural projections to the brain lack spatial order. Second, Menaker & Tosini (1996) propose that when animals become nocturnal, they reduce the number of their photoreceptors, so that exclusive retinal photoreception for the photoperiodic timer in mammals is ultimately due to their furtive nocturnal habits when they coexisted with ruling reptiles. Nocturnal geckos, snakes, alligators, owls, and benthic hagfish lack parietal eyes. Apparently, it is not nocturnality, per se, that matters; rather it is the photic environment under which animals have evolved that is ultimately responsible for reliance on extraretinal photoreceptors used in photoperiodic regulation of seasonal activities in vertebrates.

After interpretation of day length, the go/no-go photoperiodic response is initiated from the brain via hypothalamic inhibitory or releasing factors (peptides) that are transported to the anterior pituitary via the hypothalamic-hypophyseal portal system (Turner & Bagnara 1971, McNamara 2003). Tropic hormones from the anterior pituitary then control the expression of growth, molting, color, pelage, development, and reproduction. In mammals, photoreception from the retinal ganglion cells is transmitted electrically via the suprachiasmatic nucleus to the pineal that synthesizes and releases melatonin (5-methoxy, *N*-acetyltryptamine). Melatonin production is inhibited by light and proceeds in darkness, suggesting that day length signals are encoded in the duration of nocturnal melatonin secretion and decoded in melatonin target cells to provide responses associated with day length (Goldman 2001). For other vertebrates, the pineal and melatonin can play a role in circadian rhythmicity (Cassone 1998), but melatonin does not appear to be a crucial component of photoperiodic response (Goldman 2001, Mayer et al. 1997, Underwood & Goldman 1987), except

for photoperiodic control of seasonal variation in bird song (Bentley et al. 1999, MacDougall-Shackleton et al. 2001).

Chondrosteian, holosteian, and teleostean fish. We found no studies of photoperiodism in chondrosteian (paddlefish, sturgeon, *Polypterus*) or holosteian (gar pike, bowfin) fish. Photoperiodism is widespread among teleostean (higher bony) fish and has been studied in at least nine orders. In various species, photoperiod may provide the go/no-go signal for seasonal dormancy (Podrabsky & Hand 1999) as well as migration, sexual maturation, and associated physiology and behavior in migratory fish (Bromage et al. 2001). Fish with short gonadal maturation cycles generally respond positively to a single constant day length; fish with long gonadal maturation cycles usually require sequentially changing day lengths (Bromage et al. 2001). Particularly in long-lived, iteroparous fish, step-up or step-down transitions in photoperiod set the phase of the circannual rhythm (Davies & Bromage 2002, Duston & Bromage 1986, Holcombe et al. 2000, Randall et al. 1998). Reproduction is then controlled by an endogenous circannual rhythm that, under natural conditions, is entrained by seasonal changes in day length (Randall et al. 1998).

Photoperiodism has been studied primarily in game, commercial, or farmed fish, especially in salmonids (Bromage et al. 2001), where photoperiod “is regarded as the major proximate cue which adjusts the seasonal timing of reproduction” (Taranger et al. 1998, p. 403). In salmonids, photoperiod provides the go/no-go stimulus for smoltification and migration to sea and for the initiation of gonadogenesis and migration back to freshwater for spawning (Clarke et al. 1994, Quinn & Adams 1996). Smolting and sexual maturation are likely gated events in a circannual cycle so that if some size or physiological threshold is not reached during the circannual window, smolting or sexual maturation may be delayed for a year (Arnesen et al. 2003, Duston & Saunders 1990). Once a threshold size is reached, photoperiod determines the initiation of sexual maturation, which may take place at sea months before final spawning in freshwater; conversely, the timing of spawning itself is more affected by stream flow and temperature, which provide indicators of immediate environmental conditions at the spawning sites (Baras & Philippart 1999, Dabrowski et al. 1996, Davies & Bromage 2002, Huber & Bengston 1999). In general, the importance of photoperiod as the critical go/no-go determinant of sexual maturation increases with time and distance between the initiation of sexual maturation or migration and actual spawning (Clarke et al. 1994, Quinn & Adams 1996).

Sarcopterygian (lobe-fin) fish. We know of no studies on photoperiodism in coelacanth and only one among the Dipnoi (lungfish) where the onset of spawning in the Australian lungfish *Neoceratodus forsteri* is controlled by increasing day lengths of spring (Kemp 1984).

Amphibians. “The role of photoperiod in the control of amphibian reproduction is inconclusive due to the limited number of studies available” (Pancharatna & Patil 1997, p. 111). In addition, many of the available studies are inconclusive because they use tropical animals that, at their native latitudes, receive little change in annual day

length to serve as a cue (Pancharatna & Patil 1997, Saidapur & Hoque 1995) because they use animals from a commercial source or from otherwise unknown localities (Delgado et al. 1987, de Vlaming & Bury 1970, Eichler & Gray 1976, Inai et al. 2003, Jacobs et al. 1988, Willis et al. 1956, Wright et al. 1988), or because they use only extreme light regimens unlikely to be found in the subject's native habitat (Delgado et al. 1987, Eichler & Gray 1976, Saidapur & Hoque 1995) or that produce deleterious effects (Rastogi et al. 1978). In two studies of the effects of photoperiod on weight gain in *Rana pipiens*, tadpoles were provided enough food "to last the entire daylength" (Wright et al. 1988, p. 316) so that it was not clear whether accelerated development and metamorphosis on longer than shorter days was due to day length as an environmental signal or simply light-dependent feeding behavior.

A good example of amphibian photoperiodism in an ecological context is provided by *Rana temporaria* in Scandinavia (Laurila et al. 2001). In northern populations that have a strictly limited growing season, photoperiod provides the go/no-go signal for the impending winter; in the south where winter comes later and there is greater developmental flexibility, photoperiod provides a modulating effect on temperature-dependent processes.

At ecologically relevant photoperiods in amphibians of known geographic origin, photoperiod often has a modulating effect on temperature-dependent processes (de Vlaming & Bury 1970, Rastogi et al. 1976). In at least one anuran (Rastogi et al. 1976) and one urodele (Werner 1969), the combined effects of warm temperatures and long days could prevent testicular regression, so it would appear that a refractory period is not obligatory among amphibians. We are therefore left with the questions of how frequently a true photorefractory state occurs in amphibians, whether a refractory state can generate a circannual rhythm, and whether photoperiod is as effective in setting that rhythm as it is in teleosts (Bromage et al. 2001), birds (Dawson 2002), and mammals (Goldman 2001).

Turtles, snakes, and lizards. Photoperiodism in these reptiles may affect seasonal development either directly by regulating the timing of reproduction or indirectly by modifying thermal behavior and thermal preferences, thereby modifying temperature-dependent physiological processes. However, all the studies we reviewed concerned animals collected directly from the field and were not run through two generations to remove maternal and other field effects.

In turtles, long days induce an increase in critical thermal maxima and a preference for warmer temperatures (Graham & Hutchison 1979, Hutchison & Maness 1979, Kosh & Hutchison 1968). Long days therefore act as an anticipatory cue to pre-acclimate turtles for future summer heat in at least two ways. First, the direct effects of photoperiod on critical thermal maxima are equivalent to a 3°C–4°C increase in acclimation temperature. Second, by inducing a preference for warmer temperatures during early afternoon at close to the daily thermal maximum, long days are actually accelerating direct thermal acclimation (R. Huey, personal communication). To our knowledge, there are no studies determining the effect of photoperiod on the timing of reproduction or hibernation, or testing for circannual rhythms in turtles.

Zugunruhe: migratory
restlessness

In snakes, we found no well-designed study of photoperiodism. The one study we did find (Hawley & Aleksiuk 1976) used an inappropriate long day for testing for a photoperiodic effect on reproduction.

In lizards, experimental biochronometry has focused largely on circadian (daily) rhythms and not photoperiodism. Photoperiodism in lizards has been studied primarily in the green anole *Anolis carolinensis*, in which photoperiod appears to play two roles. First, long days in summer sustain testicular development and short days in the fall induce regression of the testes, reducing or eliminating the ability of warm temperature to promote spermatogenesis. Second, long days in the spring initiate an increase in feeding and growth, leading to the onset of reproduction (Fox & Dessauer 1957; Licht 1966, 1967, 1973).

Photoperiod can serve as a seasonal modulator of temperature-dependent processes in lizards. With increasing latitude, photoperiod has an increasing influence on metabolic rate (Angilleta 2001), on growth rate (Uller & Olsson 2003), and on ability to maintain a constant body temperature with increasing temperature in the spring (Lashbrook & Livezey 1970). Given their tendency to hibernate in sites with minimal photic or thermal cues, temperate-zone lizards might be expected to rely on a circannual clock for the timing of seasonal activities (Gwinner 1986). Long days retard and short days advance the reproductive cycle of *Cnemidophorus* (Cuellar & Cuellar 1977), but otherwise the role of photoperiod in setting the circannual rhythm of lizards remains untested and unknown.

Birds. “In birds, the annual change in daylength is the most important environmental cue used for synchronizing breeding moult, and migration with recurrent seasonal fluctuation in environmental conditions” (Coppack & Pulido 2004, p. 131). Temperate birds must coordinate several key events into their phenology, principally reproduction, molting, and migration (Dawson et al. 2001, Dawson 2002, Gwinner 1996). These processes are mutually exclusive energetic activities and are sequentially orchestrated in the seasonal life history of birds, both in nature and as a circannual rhythm under constant conditions. In addition, birds are constrained by the energetics of flight, which places a premium on healthy flight feathers and low body mass. Consequently, the difference in mass between reproductive and nonreproductive gonads may differ by a factor of 100, and molting usually takes place after reproduction and before migration (Dawson et al. 2001, Dawson 2002).

In birds, gonadal development begins early in the season, progresses gradually, and ceases abruptly prior to molting. The late-summer molt then marks the termination of the breeding season and provides the seasonal link to migration. Prior to migration, birds become more active and exhibit directional preferences in orientation cages provided with an artificial sun or night sky. This migratory restlessness is referred to as Zugunruhe and can be quantified in controlled environments to estimate the onset, duration, intensity, and directionality of migration.

In passerines such as starlings and sparrows, increasing day lengths of spring initiate gonadal maturation and breeding (Dawson et al. 2001, Dawson 2002, Gwinner 1996). The longer days of summer induce a photorefractory state in which reproductive processes are no longer sustained by long days and the gonads regress rapidly

to an essentially prepuberty condition. Following the summer molt, short days of autumn and winter lead to a dissolution of refractoriness and birds again become responsive to increasing or long days during the late fall or early winter.

Photoperiod provides “the most important zeitgeber [setting agent] of circannual rhythms” (Gwinner & Helm 2003, p. 83). Circannual clocks enable birds to keep track of time in unvarying tropical day lengths, and during fall and spring migration through zones of rapidly changing day length (Gwinner 1986, 1996). Under constant temperature and photoperiod, both the duration and direction of Zugunruhe in orientation cages have been observed in some birds to correspond to the mid-migration changes in migration direction of wild populations. Hence, circannual rhythmicity may account for the accurate migratory pathways of even naïve birds and provide an internal temporal reference for course changes (Helm & Gwinner 2006).

Mammals. “Photoperiodic information has been shown to be the strongest synchronizer of seasonal functions in most species” of mammals (Hofman 2004, p. 63). In addition to regulating annual reproductive cycles, photoperiod can control the timing of seasonal shedding and change in color and thickness of fur (Farner 1961), tendency to enter torpor (Heideman et al. 1999, Lynch et al. 1981), investment in nest insulation (Heideman et al. 1999, Lynch et al. 1981), temporal niche partitioning in reproduction between sympatric congeners (Dickman 1982), and embryonic diapause in which implantation of the zygote is delayed for varying durations on the basis of photoperiod (Farner 1961, McConnell et al. 1986, McConnell & Tyndale-Biscoe 1985, Renfree et al. 1981, Thom et al. 2004, Tyndale-Biscoe 1980). The incidence of photoperiodically induced gonadal regression in mice (*Peromyscus*) (Heideman et al. 1999, Lowrey et al. 2000, Lynch et al. 1981, Sullivan & Lynch 1986) and embryonic diapause in mustelids (Thom et al. 2004) increases with latitude.

Temperate mammals may be short-day (early spring) or long-day (spring and summer) breeders. Both short-day and long-day breeders may go through a period of photorefractoriness (nonresponsiveness to day length) that may interact with circannual rhythmicity. Long-day breeders cease reproduction either through the action of decreasing day lengths or through the action of long days, themselves inducing a photorefractory state (inability of long days to sustain reproduction) followed by gonadal regression. In both types, prolonged exposure to short days renders them refractory to short days and allows for the initiation of gonadal maturation (Goldman 2001). “No mammalian species are known to become refractory exclusively to long days. Mammals become refractory either to short days, or to both short and long days” (Goldman et al. 2004, p. 132).

As in birds (above), photoperiod sets the timing of the circannual clock among a wide variety of mammals (Goldman 2001, Gwinner 1986). The circannual component of mammalian reproductive cycles may be especially important for high-latitude species where the season favorable for reproduction is highly restricted, where animals experience constant light in the summer, and where individuals may hibernate under relatively constant conditions for over six months of the year.

Zeitgeber: an external cue that sets the timing of or entrains an internal, otherwise self-sustained rhythm

CONCLUSIONS

Being in the right physiological, developmental or reproductive condition at the right time and place is an essential component of fitness in seasonal environments. A wide variety of vertebrates and invertebrates in marine, freshwater, and terrestrial habitats use the day length to anticipate and prepare for seasonal transitions or events in their life histories. Several generalizations can be made about photoperiodism in animals:

1. Unlike temperature or rainfall, the annual change in day length is invariant from year to year, and day length therefore provides a highly reliable anticipatory cue for future or distant seasonal conditions.
2. A specific photoperiodic response is based on selection through evolutionary time for the optimal seasonal time to develop, migrate, reproduce, or go dormant.
3. Photoperiodism regulates a go/no-go response that initiates a cascade of physiological, developmental, or reproductive processes that are generally irrevocable within the lifetime of the individual or are not reversed before completion of the seasonal event under selection.
4. In ectotherms, photoperiodism may act in concert with temperature to regulate subsequent continuous rate processes and thereby fine-tune the actual timing of the seasonal event in a thermal environment that varies from year to year.
5. Photoperiod tends to provide the most important cue for events that are distant in time or space; temperature, food, and other ecological conditions become more important closer to the actual event itself.
6. Animals may respond to either absolute or changing day lengths; reliance on absolute day length is more prevalent in short- than long-lived animals.
7. Critical photoperiod, threshold day length, or the incidence of photoperiodism within and among species tends to increase with latitude or altitude in the temperate zone.
8. Photoperiodic response within populations may be affected by circadian rhythmicity, but the seasonal photoperiodic timer and the daily circadian clock can evolve independently over seasonal, geographic gradients.

Animals use day length in conjunction with circannual rhythmicity and refractory periods to keep track of seasonal time not only at temperate latitudes but also at tropical overwintering localities with constant day length, during migration through zones of rapidly changing day length, during polar summers with constant light, and in winter hibernacula or during polar winters with constant darkness.

Day length is perceived through either optic (compound eye, retina) or extraoptic (ocelli, pineal, brain) photoreceptors. In vertebrates, primary photoreception is by nonvisual irradiance detectors in the retina, pineal, or hypothalamus. In all animals, day length is assessed within the brain and transmission of the photoperiodic signal to target organs involves peptide hormones at some step in the pathway (with the possible exception of melatonin's effect on song centers of the avian brain). Melatonin serves as an interval signal for mammalian photoperiodism but does not appear to play a significant role in photoperiodic response of other vertebrates except, again, for avian song.

Most importantly, photoperiodic response is a crucial component of fitness that cannot be overlooked when considering the present distribution of animals, life-history evolution, range expansion or contraction, invasiveness of agricultural pests or vectors of disease, outcrossing of managed populations for the maintenance of genetic variability, the introduction or transplantation of species for agricultural or biological control or for biological conservation, and the potential persistence of populations confronted with rapid climate change.

PREDICTIONS FOR RAPID CLIMATE CHANGE

Recent, rapid climate change has resulted primarily in warmer winters rather than warmer summers, and the rate of winter warming has increased with latitude (IPCC 2001, 2007). Warmer winters have resulted in earlier springs, later onset of winters, and longer growing seasons. However, at any locality on Earth, climate warming does not alter day length. Animals from rotifers to rodents use this high reliability of day length to time the seasonal events in their life cycles that are crucial to fitness in temperate and polar environments: when to develop, when to reproduce, when to enter dormancy, and when to migrate. Climate warming is changing the optimal timing of these events and, consequently, is imposing selection on the photoperiodic response used to time them. For example, recent genetic shifts in photoperiodic response in the pitcher-plant mosquito have occurred over as short a time span as five years (Bradshaw & Holzapfel 2001a, 2006).

By contrast, there are, to our knowledge, no examples of genetic increases in thermal optima or heat tolerance associated with climate warming in any animal. We therefore predict that, when confronted with continued, rapid climate change, the differential ability of animals to track that change, and hence the composition of future biotic communities, will depend on the evolvability of their respective photoperiodic responses (Bradshaw & Holzapfel 2001a, 2006, 2007).

FUTURE ISSUES

1. How prevalent are photoperiodism and circannual rhythmicity among invertebrates other than arthropods?
2. How many times has photoperiodism evolved? For instance, did it arise independently in echinoderms and vertebrates or was there a common deuterostome origin?
3. What is the genetic basis of photoperiodic response within populations, how does this variation respond to selection along climatic gradients, and does it relate to the circadian clock?
4. Is there a central circannual clock or is circannual rhythmicity simply the concatenation of multiple, long-term physiological processes?
5. What are the relative contributions to fitness of the photoperiodic timer and the circadian clock in natural populations?

6. How well do rates of evolution (genetic change) in photoperiodic response track rapid climate change among diverse animal taxa?

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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