Light, Time, and the Physiology of Biotic Response to Rapid Climate Change in Animals

William E. Bradshaw and Christina M. Holzapfel

Center for Ecology and Evolutionary Biology, University of Oregon, Eugene, Oregon 97403-5289; email: mosquito@uoregon.edu

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seasonality, photoperiodism, temperature, hormonal regulation, dormancy

Abstract

Examination of temperate and polar regions of Earth shows that the nonbiological world is exquisitely sensitive to the direct effects of temperature, whereas the biological world is largely organized by light. Herein, we discuss the use of day length by animals at physiological and genetic levels, beginning with a comparative experimental study that shows the preeminent role of light in determining fitness in seasonal environments. Typically, at seasonally appropriate times, light initiates a cascade of physiological events mediating the input and interpretation of day length to the output of specific hormones that ultimately determine whether animals prepare to develop, reproduce, hibernate, enter dormancy, or migrate. The mechanisms that form the basis of seasonal time keeping and their adjustment during climate change are reviewed at the physiological and genetic levels. Future avenues for research are proposed that span basic questions from how animals transition from dependency on tropical cues to temperate cues during range expansions, to more applied questions of species survival and conservation biology during periods of climatic stress.

INTRODUCTION

Phenotypic plasticity: the ability of an individual organism to change its physiological, behavioral, developmental, or morphological phenotype, usually in response to a variable environment

Evolution: a change in gene frequencies in a population, whether due to a response to selection, to genetic drift, to immigration, or to emigration. Evolution is a property of populations, not individuals

Fitness: the ability of an individual to increase its representation in future populations

Physiology provides the functional link between the genome and the environment. Physiological response to the environment can take place at several levels, including phenotypic plasticity at the individual level and actual evolution, i.e., genetic change at the population level. Recent, rapid climate change is proceeding at a pace that is unprecedented since the end of the Younger Dryas, 12,000 years ago (1). Earth surface temperatures are warmer now than they have been in the past 1200 years (2), and atmospheric CO_2 levels are higher now than they have been in 125,000 years (3). Present climate warming is proceeding faster at temperate and polar latitudes than at equatorial latitudes (4, 5). The consequences of increasing temperatures have direct effects on the nonbiological (abiotic) world: Mountain and polar glaciers are retreating, polar ice is melting, and sea levels are rising (5, 6). This direct effect is dramatically illustrated by the retreat of the Columbia Glacier in Alaska over the past 25 years (**Figure 1**).

The natural assumption is that temperature is having an analogous, direct, and detrimental effect on animals. However, living organisms are not glaciers, and to assume that the proximate biological response to rapid climate change is the same as that of the abiotic world is, at best, unwarranted. To understand biological responses to climate change, it is necessary first to identify these responses and only then to elucidate their mechanisms. To begin, biotic responses to recent rapid climate change fall into two principal categories: the poleward advance of species' ranges and altered timing of seasonal events in plant and animal life histories (7–12). Herein, we examine the physiological basis of biotic response to rapid climate change, focusing on the temperate and polar zones wherein lie two-thirds of the Earth's landmass. We examine geographical patterns of light and temperature, how climate warming alters these patterns, and how these altered patterns impose selection on populations. We discuss the relative roles of light and temperature experimentally in determining fitness of populations. We proceed by providing examples of physiological and hormonal cascades likely to change as a consequence of this selection and by presenting documented examples of evolutionary (genetic) change in populations. We conclude with suggested avenues of future experimental research.

THE ABIOTIC WORLD

The rotation of the Earth about its own axis gives rise to the daily changes in light and temperature; the tilt of the earth relative to its plane of rotation about the sun gives rise to the annual changes in light and temperature and, consequently, the changing seasons. Along the equator there is no annual change in day length (**Figure 2**), but as one proceeds

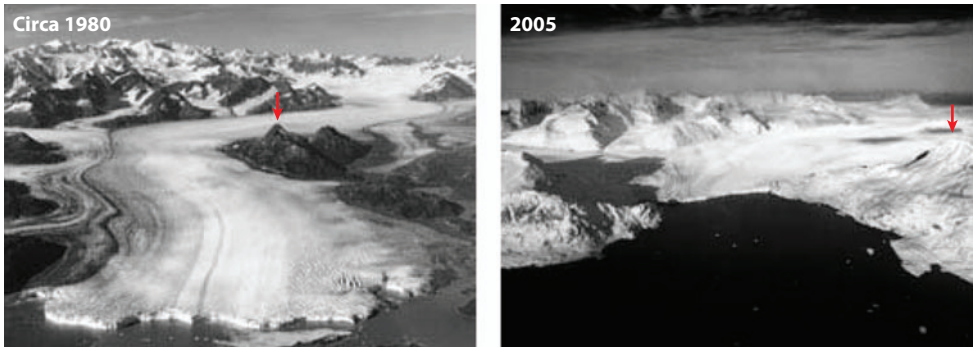

Figure 1

Retreat of the Columbia Glacier over 15 km between 1980 and 2005. The arrow indicates the same point, 25 years apart (courtesy of NASA, owner of image: **http://visibleearth.nasa.gov/**).

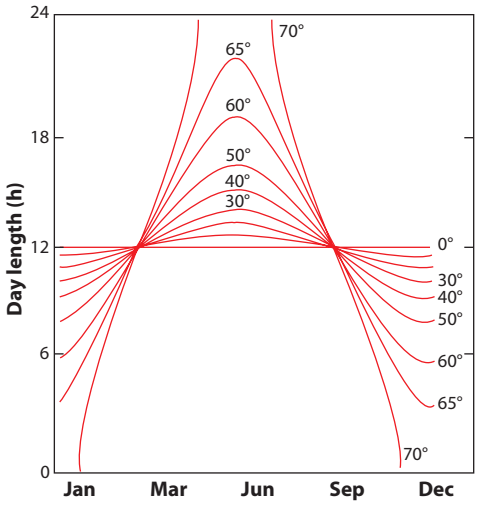

Figure 2

Geographic and seasonal variation in day length (sunrise to sunset) at different latitudes (°N) in the Northern Hemisphere (13). Climate warming does not change these relationships.

toward the poles, the annual change in day length increases. This pattern of increasing summer day lengths and decreasing winter day lengths with increasing latitude is unaffected by climate change. The day length at a given place and date on the planet is the same today as it was 10,000 years ago and will be 10,000 years into the future. Hence, the annual change in day length closely parallels the annual change of the seasons and has continued to do so through evolutionary time.

Because of the tilt of the Earth about its axis of rotation, the Sun's rays fall at ever more acute angles as one goes toward the poles and thereby impart less heat to the surface of the Earth. Consequently, mean annual temperature decreases and annual change in temperature increases with latitude. **Figure 4** (below) shows the isotherms (lines of equal temperature) of mean monthly temperature for eastern North America from the Gulf of Mexico to the Canadian border. Three important observations concern the isotherms in **Figure 4**. First, summer isotherms are far apart, indicating a shallow thermal gradient; summer temperatures in Minnesota are not greatly different from those in Mississippi. Second, winter isotherms are close together, indicating a steep thermal gradient; winter temperatures in Minnesota are very different from those in Mississippi. Third, the 15°C isotherm defines a summer growing season of 10.5 months along the Gulf of Mexico (30°N) but only 3 months near the Canadian border (48°N). These observations mean that the climatic gradient of eastern North America is primarily one of winter cold, not summer heat, and that the growing season available for development and reproduction declines with increasing latitude.

Unlike light, the geographic and annual patterns of temperature are changing with global warming. Climate warming is proceeding faster in the winter than in the summer and is changing faster with increasing latitude (4, 5). Warmer winters are resulting in earlier springs, later onsets of winter, longer growing seasons, and a reduction in the severity and duration of winter cold without appreciably increasing summer heat. In the Northern Hemisphere, northern regions are becoming more southern-like; in the Southern Hemisphere, southern regions are becoming more northern-like. In short, the direct effects of temperature are changing the nonbiological world in ways that few of us had previously considered. The question then becomes, How are animals and plants responding to this new world, and what environmental cues are driving biological responses to rapid climate change?

THE BIOTIC WORLD

Only model organisms in the laboratory live in a world of endless summer. In nature, fitness is defined by the ability to exploit the favorable seasons, the ability to avoid or mitigate the unfavorable seasons, and the ability to switch from one lifestyle to others at the appropriate times. Exploitation of the favorable seasons involves life-history traits that contribute to positive population growth, e.g., high survivorship, high fecundity, and short generation times. Avoidance of the unfavorable season involves escape in time or space through dormancy or

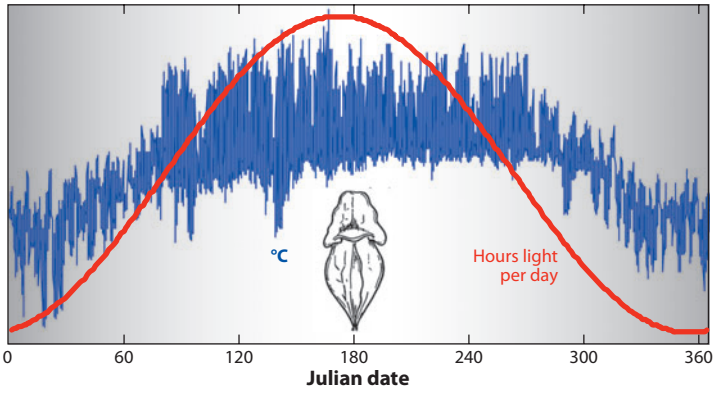

Figure 3

Annual change in day length (*red*) and temperature (*blue*) measured every 2 h for a year inside the leaf of a pitcher plant at 30°N. The mosquito *Wyeomyia smithii* completes its preadult development only within these water-filled leaves and uses the length of day to program the onset, maintenance, and termination of larval dormancy. Mosquitoes at this latitude have all entered dormancy by day 300, well in advance of winter cold (17). Temperatures are from Bradshaw et al. (14); day lengths are compiled from tables in Beck (18).

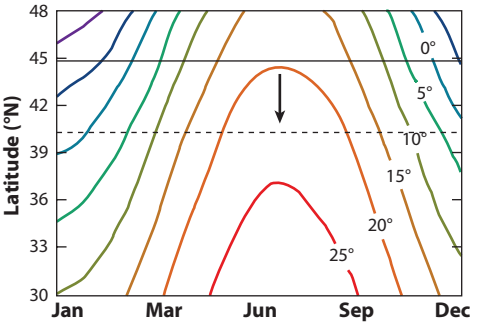

Figure 4

Isotherms for mean daily temperature in central and eastern North America from the Gulf of Mexico to the Canadian border (14). Global warming (*arrow*) is making the thermal year of northern latitudes (*solid gray line*) more southern-like (*dashed gray line*).

migration. The trick is to time the transition between these two lifestyles so as to maximize the first without jeopardizing the second. Seasonal transitions require advance preparation. Animals do not wait for the arrival of summer to begin development, vernal migration, or maturation of the gonads, nor do they wait for the arrival of winter to accumulate nutritional reserves, enter dormancy, or migrate. Rather, animals from rotifers to rodents use the length of day to anticipate and prepare in advance for future seasonal change (15, 16). Environmental conditions such as temperature, moisture, or resources can vary dramatically from day to day and year to year, but as we noted above, the seasonal change in day length remains highly consistent over evolutionary time (**Figure 3**).

Adaptation: genetic change in a population due to natural selection, leading to improvement of some function or increased suitability to some aspect of the environment. Adaptation is a property of populations; individuals do not adapt

Fitness in Nature

As discussed above, fitness in temperate and polar environments depends upon the ability to exploit the summer growing season, the ability to avoid or mitigate winter conditions, and the ability to switch between the two lifestyles at the optimal time of year. As climates change with geography, so also do the day lengths that organisms use to program seasonal changes in their life cycles. Northern climates have shorter growing seasons and winter comes earlier in the year than in the south (15°C isotherm in **Figure 4**). Consequently, to enter dormancy earlier in the year, a northern population would have to use a longer day length to switch from active development to diapause. Because both season length and temperature vary with latitude (**Figure 4**), the question remains as to whether response to day length or temperature is driving adaptation to the climates experienced at different latitudes. To answer this question, Bradshaw et al. (14) first defined fitness in a seasonal environment by *Ry*, the year-long cohort replacement rate integrating performance through all four seasons (**Figure 5**).

Second, using climate-controlled rooms, they compared fitness (*Ry*) of northern populations reared in a northern photic and thermal year with that of the same populations reared in a northern photic year, but with a southern thermal year (**Figure 6*a***), and observed a 47% increase in the warmer environment. Hence, the warmer southern environment turned out to be benign and advantageous to the northern animals; transplanting to the southern thermal year actually improved fitness of northern animals in the warmer thermal environment. Although this result was unexpected, it was confirmed by Deutsch et al. (19), who showed

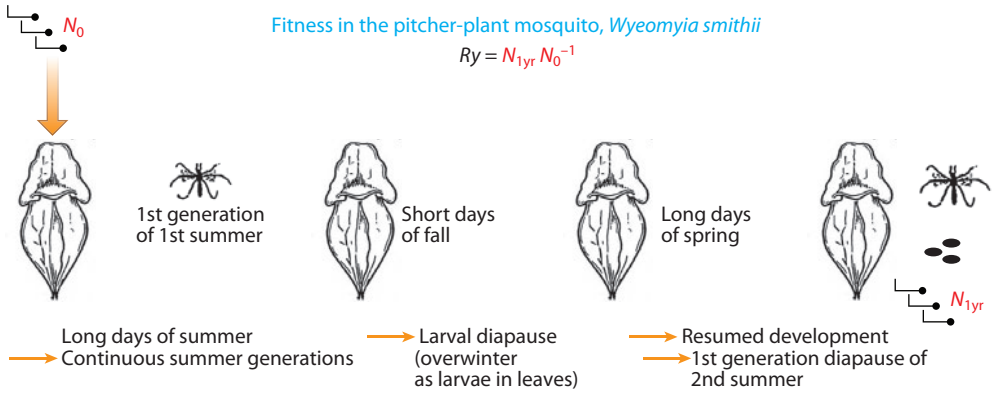

Figure 5

Ry, the year-long cohort replacement rate, integrates fitness through all four seasons. Fitness was determined in the leaves of intact pitcher plants inside computer-controlled environment rooms capable of programming daily and annual changes in temperature, humidity, and day length to simulate any climate from the tropics to the arctic. Feeding regimens followed the natural prey-capture pattern of pitcher plants in the field.

that climate warming through the next century is actually expected to improve fitness (*r*) of ectotherms at temperate and polar latitudes.

Third, they determined *Ry* in the same benign southern thermal year but, instead of the northern photic year, programmed a southern photic year and observed an 88% loss of fitness in the southern as compared with the northern photic year. The reason for the dramatic loss of fitness in response to the southern photic year is shown in **Figure 6*b***. In the benign southern thermal environment with typical northern summer day lengths, development proceeded through the summer, and the northern populations increased in numbers until the short days of fall induced diapause. In the benign thermal

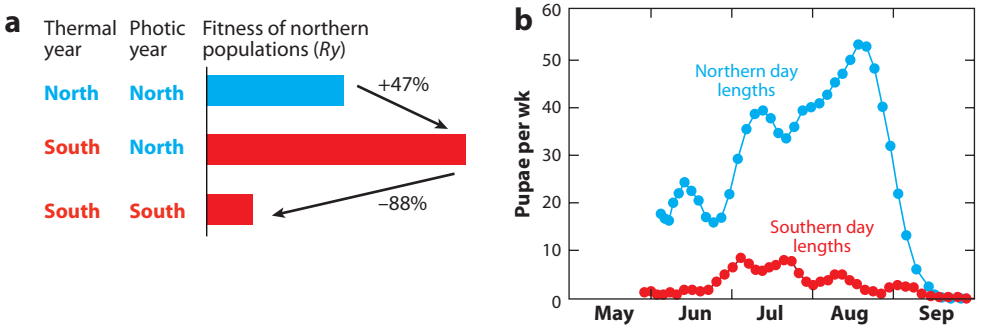

Figure 6

Fitness of northern *Wyeomyia smithii* populations in the leaves of intact pitcher plants. Northern mosquitoes were exposed to their native photic and thermal year, to a southern thermal year with a northern photic year, or to a southern thermal and southern photic year. The thermal year consisted of daily and annual fluctuations in temperature based on temperatures recorded in nature; the photic year consisted of annual fluctuations in day length, including both civil twilights measured in pitcher-plant leaves (20). As in nature, the thermal day lagged the photic day by 3 h, and mosquitoes were fed freeze-dried adult *Drosophila* to mimic the timing of prey capture by host leaves in nature (17). (*a*) Fitness (*Ry*) of northern mosquitoes in their native or in southern thermal and photic years. (*b*) Rate of pupation of northern populations in the southern thermal year but provided either with the typical longer, northern summer day lengths (*blue*) or with shorter, southern day lengths (*red*) (14).

Photoperiodism: the ability to assess the length of day or night to regulate (usually seasonal) physiology, development, morphology, or reproduction

Circannual rhythm: a rhythm with an oscillatory period of approximately a year that is sustained in a constant environment and is capable of being set by external cues, usually photoperiod

Refractory period: inability to respond to day length, herein, inability to respond to long days. Refractoriness may be induced spontaneously or by long days themselves and may be terminated spontaneously or in response to short days or low temperatures

Circadian rhythm: a temperature-compensated rhythm with an oscillatory period of approximately a day that is sustained in a constant environment and is capable of being set by external cues, usually light

environment with shorter southern day lengths, day lengths were not long enough to avert diapause, and most of the larvae did not develop. Instead, these larvae passed the warm summer, the fall, and the winter in diapause. The few larvae that survived winter and developed the following spring had greatly reduced fecundity. Hence, the correct response to day length, even in a thermally benign environment, is crucial for maintaining fitness in temperate and polar environments.

Importantly, the middle experiment in **Figure *6a***, representing combination of a southern thermal year and a northern photic year, is not possible in nature—unless the species in question is first demonstrated not to be photoperiodic (**Figures 2** and **4**). In transplants in nature from a northern to a southern locality in nature, the results could readily lead to the erroneous conclusion that the loss of fitness in the northern populations was due entirely to drought or heat stress and not a maladaptive response to day length as in Reference 21. In nature, transplants between latitudes will always and unavoidably confound the effects of drought or temperature with response to day length and, hence, cannot be used to infer potential performance of populations due to rapid climate change. For example, in stonechats (*Saxicola torquata*), European populations have a long breeding season, and Siberian populations, experiencing only a brief summer, have a short breeding season. When each population was reared separately in outdoor aviaries in southern Germany, each population retained its photoperiodically timed breeding season, and females of both populations produced a high proportion of fertile clutches. However, when European females were mixed with Siberian males, they produced a high proportion of infertile clutches, except at the time of year the Siberian males were in breeding condition (22). Analogously, although the introduction of European rabbits to Australia was highly successful at cooler (southern) latitudes, their spread toward warmer (northern) latitudes was inhibited by their inherited European response to day length (23). Finally, in order to replace an extinct herd of Czechoslovakian ibex, breeding stock was imported first from Austria (same latitude) and later from Turkey and Sinai (more southern latitudes). The first introduction from the same latitude was successful, but the otherwise fertile north-south hybrids rutted in the early fall instead of the winter, the kids of these hybrids were born in midwinter instead of spring, and the entire population died out (24). Hence, results of experiments with mosquitoes under carefully simulated natural year-long environments are reflected in outdoor aviaries and species or populations introduced into exotic photic environments: maladaptive response to day length leads to reduced fitness or extinction of populations.

How Animals Can Use Light: Photoperiodism, Photoperiod, and Circannual Rhythms

The above discussion underscores the central importance of the timing of essential life-history events to fitness in temperate and polar seasonal environments. Seasonal timing in animals usually involves photoperiod (the duration of light in a light/dark cycle), photoperiodism (the ability to use the length of day or night to regulate seasonal behavior or physiology), and the circannual clock (an internal, self-sustained clock with a period of oscillation of approximately a year), coupled with a refractory period when animals do not respond to day length.

Photoperiodism. Photoperiod regulates go/no-go responses that are usually irrevocable within the lifetime of an individual or are not reversed before completion of the seasonal event in question (15). This seasonal go/no-go response is in sharp contrast to the responses orchestrated by the daily circadian clock, whose functions are fully reversible (can be re-entrained) on a day-to-day basis (25–27). There are two primary components of photoperiodism (28): the photoperiodic timer that assesses the length of day or night (15) and the photoperiodic counter that accumulates or

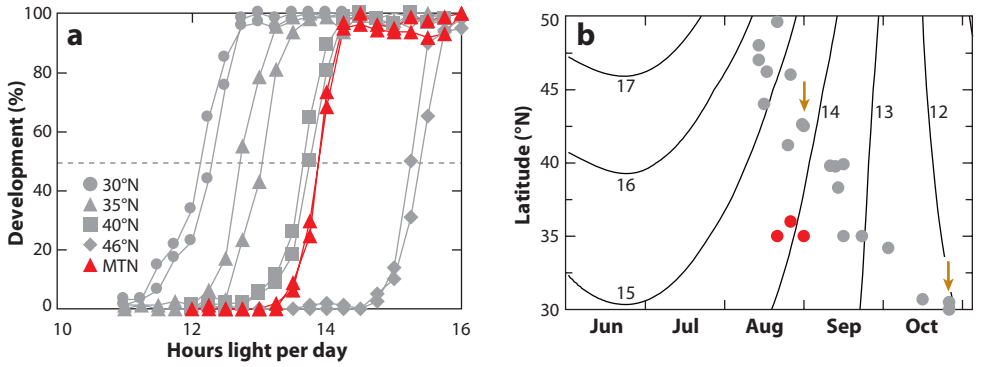

Figure 7

Geographic variation in photoperiodic response and dates of diapause initiation in *Wyeomyia smithii* populations from eastern North America. MTN are mountain populations at 900–1000 m at 35°N and are plotted in red. (*a*) Photoperiodic response curves. The dashed line indicates 50% development; the critical photoperiod is the number of hours of light per day where the dashed line intersects a given photoperiodic response curve. (*b*) Critical photoperiods plotted on a contour of day length (sunrise-sunset plus two civil twilights). The arrows indicate populations where entry into diapause is known: Populations at 30°N are in diapause by November 1 (30); populations at 42.5°N enter diapause in late August (31). Hence, critical photoperiods determined in the laboratory provide an accurate proxy for date of diapause initiation. Gray dots indicate lowland populations.

counts the number of long- or short-day cycles that the animal has experienced (29). Photoperiodism is assessed by exposing animals to various day lengths in a 24-h cycle, generating a photoperiodic response curve and defining the critical photoperiod as the inflection point of this curve (**Figure 7*a***). As one proceeds from south to north, winter arrives earlier in the year when days are longer. Concomitantly, the photoperiodic response curve is shifted toward longer day lengths (**Figure 7*a***), resulting in earlier entry into diapause at more northern latitudes (**Figure 7*b***).

The photoperiodic counter accumulates the required number of short-day cycles to initiate diapause. In the mosquito *Wyeomyia smithii*, the onset, maintenance, and termination of diapause are all regulated by day length, and coordination of photoperiodic response is both geographic and genetic. Southern populations with shorter critical photoperiods (a measure of the photoperiodic timer) require more short days to enter diapause and fewer long days to terminate diapause (measures of the photoperiodic counter) than do northern populations (29, 32, 33). Analogously, within populations, genotypes with shorter critical photoperiods require more short days to enter diapause and fewer long days to terminate diapause (33). Hence, there is genetic coordination from diapause-prone to diapause-averse genotypes in the photoperiodic timer and counter both within local populations and among populations over a latitudinal climatic gradient.

Importantly, photoperiodic response is an adaptation to seasonality orchestrated by light. Response to day length is a genetically programmed physiological tool that animals use to predict future environments. If a particular response to day length results in the correct timing of seasonal events, that response will persist in a population; if a particular response to day length results in the incorrect timing of seasonal events, that response will decline in the population. Hence, going up a mountain at the same latitude, animals experience no difference in the annual change in day length but do experience progressively shorter growing seasons and, consequently, exhibit more northern responses to day length (34, 35) and enter dormancy earlier in the year (**Figure 7*b***). Indeed, one of the most robust ecogeographic "rules"

Critical photoperiod: the length of day that induces a 50% long-day response and a 50% short-day response in a population or cohort; the length of day that causes an individual to switch from a long- to a short-day response or vice versa

is that critical photoperiods increase with latitude and altitude among arthropods entering an hibernal dormancy (13, 15, 36, 37).

The photoperiodic response curves in **Figure 7*a*** require large numbers of animals and sometimes months to complete. Not surprisingly, the relationship between geography and response to day length has been studied more thoroughly in insects than in any other taxonomic group. Nonetheless, when sought, photoperiodism has been found among rotifers, gastropod mollusks, polychaete and olicochate annelids, echinoderms, fish, frogs, lizards, turtles, birds, and mammals (15). Latitude and photoperiodism are also related in vertebrates. In the frog *Rana temporaria* in Scandinavia, photoperiod provides a firm go/no-go signal for the impending winter; further south, where developmental flexibility is greater, photoperiod has a modulating effect on temperature-dependent processes (38). Among lizards, with increasing latitude, photoperiod has an increasing influence on metabolic rate (39), on growth rate (40), and on the ability to maintain a constant body temperature with increasing ambient temperature in the spring (41). Populations of the great tit, *Parus major*, from northern Italy, southern Sweden, and northern Norway require progressively longer spring day lengths to induce testicular growth in male birds (42). Among short-lived mammals, the incidence of photoperiodically induced gonadal regression in mice (*Peromyscus*) (43–46) and of embryonic diapause in mustelids (47) increases with latitude. In sum, among vertebrates, the use and intensity of photoperiodism increase with latitude as winters become more severe and the window of reproductive opportunity becomes narrower.

Circannual rhythms. Most short-lived animals with a short period of reproductive maturation rely on absolute day length to interpret time of year. Longer-lived animals, including some annelids, echinoderms, birds, and mammals, rely on a combination of absolute and changing day lengths in concert with their circannual clock and a refractory period to time their seasonal activities (15). Circannual clocks are endogenous (internal and self-sustained under constant conditions) physiological rhythms with a period of approximately a year (9–15 months). Given sufficient longevity (as well as investigator patience and funding), circannual rhythmicity may persist for many years. A single male stonechat, *Saxicola torquata*, lived for 10 years under a constant temperature, under a constant light/dark cycle, and with constant feeding. The bird exhibited a clear 10-month rhythm in gonadal cycle and molting (48). Circannual clocks are set by day length. There is no fixed critical photoperiod; rather, a given day length can be long or short, depending on the photoperiodic history of the organism. Under natural conditions, the circannual clock is set by seasonally changing day lengths. Short days in the late summer will lead to corrective advances in 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 (49–53). During the annual seasonal cycle, the circannual clock provides a gate in time during which events may take place, and if individuals are not above the threshold size or physiological condition to make a life-cycle transition, that transition is usually delayed for another year. For example, fish in the marine environment either commence sexual maturation and migration at a specific time of year or wait for a subsequent year to do so (54, 55). Hence, changing day lengths control sexual maturation by setting and interacting with the circannual clock that then triggers life-cycle transitions at the clock-coordinated time of year (52, 53, 56, 57).

In the European blackcap warbler, *Sylvia atricapilla*, the lengthening days of spring induce migration and reproductive maturation, and the long days of summer induce a refractory period during which the birds cease reproduction and commence their premigratory molt. The shortening day lengths of fall trigger autumnal migration. During the late summer and fall, the birds are refractory to long

days; during the refractory period, long days are no longer able to induce or sustain reproductive activity. The refractory period is terminated by the short days of winter, and the birds again become responsive to the lengthening day lengths of spring (48, 49, 58–60). In this case, it is the interaction of changing and constant day lengths with the circannual clock and a refractory period that result in the optimal timing of reproduction, molting, and migration in concert with changing seasonal opportunities and exigencies.

Translating Day Length into Seasonal Phenotypes: Hormones in Action

The above discussion establishes that the role of day length in regulating the timing of seasonal development ranges from irrevocable, once-in-a-lifetime go/no-go decisions to quantitative modulation of developmental rates. Hence, there must be mechanisms for the input and interpretation of day length and for the endocrinological output that effects expression of seasonal phenotypes (**Figure 8**). To illustrate the variety of input-output pathways among animals, we compare photoperiodic control of seasonal reproduction in insects, mammals, and birds.

Insects. Photoperiodic control of seasonal development at the hormonal level in arthropods is well illustrated by ovarian maturation and diapause in flies (Diptera), largely because of research related to aging in *Drosophila* and to reproductive physiology in mosquito vectors of human disease. Both *Drosophila melanogaster* (61–67) and the mosquito *Culex pipiens* (68–73) can undergo an adult ovarian diapause during which ovarian maturation ceases at a previtellogenic stage (before yolk deposition in the oocytes), lipids are sequestered, and stress resistance increases. Continuous ovarian maturation or the termination of diapause is dependent on both the insulin signaling pathway and juvenile hormone, a sesquiterpenoid secreted by the corpora allata in the ring gland of Dipterans (**Figure 9**). In combination, the insulin signaling pathway, the presence or absence of juvenile hormone from the corpora allata, and ecdysteroid from the ovaries control ovarian development (74–81).

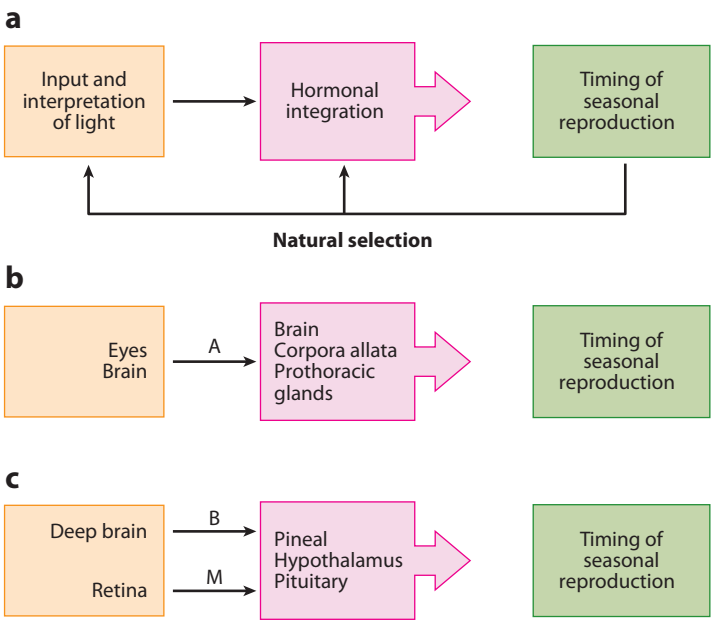

Figure 8

Input, interpretation, and hormonal integration of light to effect photoperiodic response. (*a*) Fitness is determined by how well the timing of seasonal reproduction is coordinated with seasonal changes in the environment. Deviations from optimal timing then undergo selection by the environment, and natural selection feeds back and modifies the physiological processes responsible for the timing of reproduction. (*b*) A, arthropods; (*c*) B, birds; M, mammals.

Mammals and birds. The seasonal reproductive cycle of vertebrates in general is controlled by the releasing hormones from the hypothalamus to the anterior pituitary (**Figure 10**). Gonadotropin-releasing hormone (GnRH) from the hypothalamus stimulates the release of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the anterior pituitary. LH promotes testosterone production from the testes, the production of estrogen and progesterone from the ovaries, and actual ovulation. FSH promotes sperm maturation in the testes and ovarian maturation in the ovaries (82).

In mammals, the exclusive input of light is through the retina. Electrical stimulation

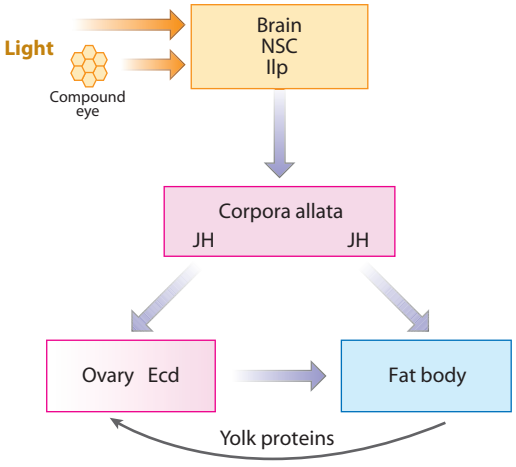

Figure 9

Control of ovarian maturation in flies (Diptera). The input of photoperiodically effective light may be either through the eyes or directly to extraoptic photoreceptors in the brain (28). A stimulatory response results in secretion of insulin-like proteins (Ilp) from the median dorsal neurosecretory cells (NSC) that, in turn, stimulate the corpora allata to secrete juvenile hormone (JH). JH acts early in ovarian maturation to stimulate yolk protein production in the ovaries and fat body and the secretion of ecdysteroid (Ecd) by the ovaries. Ecd from the ovaries then sustains yolk protein production by the fat body later in ovarian maturation.

is then relayed to the pineal gland via the suprachiasmatic nucleus, the paraventricular nucleus, and superior cervical ganglion. Electrical stimulation blocks the production of melatonin from the pineal gland so that long days result in a brief nocturnal production of melatonin and short days result in a long nocturnal production of melatonin (83). The binding of melatonin by melatonin receptor-1 in the pars tuberalis of the pituitary then stimulates the cascade of events leading to the production of gonadotropins (84, 85). In different mammals, reproduction is stimulated by either long or short days. Because deiodinase 2 (DIO2) induction by long days appears to be a common feature of long- and short-day breeding mammals (86), it is still unclear how the same melatonin signal is translated into a long- or a short-day response.

In birds, photoperiodic response is controlled mainly by light input through the orbit directly to the ventral hypothalamus (58, 59). The action of light in birds then proceeds as in mammals, stimulating the cascade of events leading to the production of gonadotropins (86–89).

Common to seasonal reproduction in arthropods, birds, and mammals is a neuroendocrine axis that begins with the input of light and terminates with secretion of a gonadotropin, be it a terpenoid in insects or a peptide in vertebrates. The role of light in this process is to initiate a cascade of physiological events that culminates in reproduction at the appropriate time of year. The initiation of these events may be separated by many months or thousands of kilometers from the actual act of mating, parturition, or oviposition, so light serves as an anticipatory cue for the timing of future important life-history events. Many physiological functions respond directly to contemporary environmental change, but the long-term, light-cued anticipation of future environments is unique to photoperiodism, whether it involves a response to absolute day length, whether it serves to set the circannual clock, or whether it serves to initiate a refractory period and then to resume time keeping at the end of the refractory period. As with life-cycle transitions in general, success is all about being at the right place at the right time (94–99). If there is an optimal time to reproduce, then there is an optimal time to initiate the cascade of neuroendocrine events leading up to reproduction. Over time, there will be stabilizing selection on the specific cues used to initiate these processes. Hence, it is the fitness attained in a future environment that imposes selection on the interpretation of light and its hormonal integration (**Figure 8*a***). Geographic variation and temporal character displacement (15) in the timing of seasonal events attest to selection in the distant past, but recent rapid climate change is also exerting contemporary selection.

Anticipatory cue: features of the current environment that permit organisms to predict and prepare for future or distant environments

From Physiology to Genetics: The Evolutionary Response to Rapid Climate Change

Historically, evolutionary change has been envisioned as a long-term process. However, there is increasing evidence that evolution can take

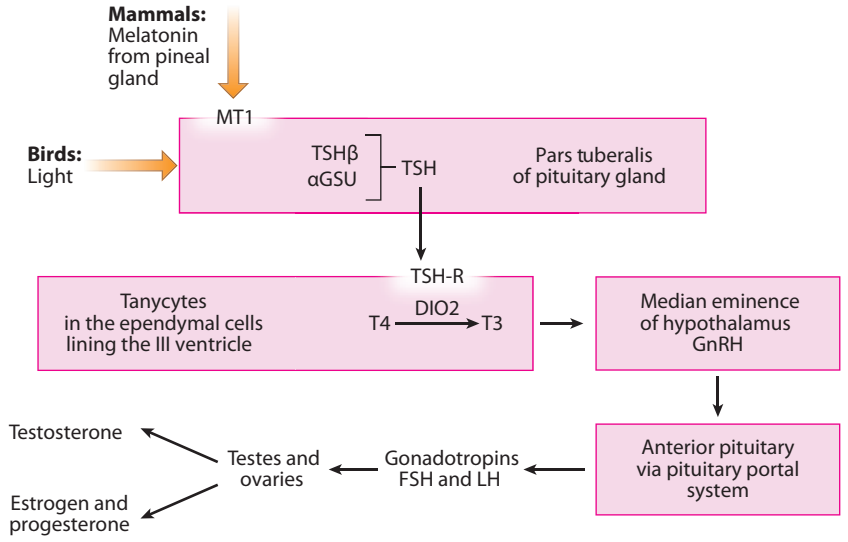

Figure 10

Transduction of light input in mammals and birds to stimulation of gonadal function. In mammals, light is perceived by the retina and is relayed electrically to the pineal gland, which secretes melatonin in proportion to night length. Melatonin is then bound by the melatonin receptor (84) in the pars tuberalis of the pituitary. In birds, light is perceived in the ventral medial hypothalamus and is communicated to the pars tuberalis by an unknown pathway. In both mammals and birds, the cascade of events leading to reproduction commences in the pars tuberalis with the transcription of the beta subunit of thyroid stimulating hormone (TSHβ), whose protein forms a heterodimer with the alpha subunit of glycoprotein hormone (αGSU) to create the active form of thyroid-stimulating hormone (TSH). TSH is transported to the nearby tanycytes in the ependymal cells lining the third ventricle, where it binds to its receptor (TSH-R) and, via a cAMP-dependent pathway, stimulates the production of deiodinase 2 (DIO2). DIO2 catalyzes the conversion of thyroxin (T4) to the bioactive tri-iodothyrynine (T3). In turn, T3 stimulates the production of gonadotropin-releasing hormone (GnRH) from the median eminence of the hypothalamus. GnRH is transported to the anterior pituitary via the pituitary portal system, stimulating the release of the gonadotropins follicle-stimulating hormone (FSH) and luteinizing hormone (LH). Pathways based on References 82 and 86–93.

place over contemporary timescales (95, 96, 100–102). As discussed above, recent rapid climate change is having very different effects in the abiotic and the biotic worlds. The major biotic responses to climate change have been the poleward expansion of species and the altered timing of seasonal events. Both of these responses impose selection on the interpretation of light and its hormonal integration. First, with polar range expansion, even if the optimal time for a seasonal event does not change between the ancestral and the new environment, the more polar habitat will present a novel photic environment (**Figure 2**), thereby imposing selection on the interpretation and integration of light. Second, altering the timing of seasonal events in situ to earlier reproduction in the spring or later migration or dormancy in the fall will likewise impose selection on the interpretation and integration of light. In general, the first response to a variable environment is through individual phenotypic plasticity. When individual phenotypic plasticity is exceeded, natural selection is exerted on the population as a whole, and evolution occurs (103). Individual phenotypic plasticity appears to be sufficient for reproductive timing of British great tits, *Parus major*, to keep pace with the progressive seasonal advance of their principal food source for feeding their young (104). However, phenotypic plasticity is not sufficient for Dutch great tits to keep pace with the seasonal advance of

their principal food source, resulting in differential reproductive success among birds with a greater or lesser range of phenotypic plasticity and therefore imposing seasonal selection within the population (105, 106). Strong contemporary selection is also evidenced by the disappearance of plants around Walden Pond that are unable to advance the timing of spring flowering rapidly (107) and by the decline in population sizes of long-distance migratory birds that are unable to advance the timing of spring arrival and egg laying at temperate latitudes (108).

In response to selection, there are now a number of examples of species or populations that are altering the timing of seasonal events in their life histories at the genetic level. Pedigree analysis has shown that 13% of the advance in parturition of Yukon red squirrels is genetic (109) and that there has been a genetic change in the degree of phenotypic plasticity in the timing of egg laying in a Dutch population of great tits (106). Comparisons of past and contemporary populations have shown a genetic shift toward earlier flowering dates in *Brassica rapa* (110); genetic shifts toward an increased number of generations; later entry into diapause; and shorter, more southern critical photoperiods in insects (95, 111). Genetic shifts toward earlier arrival, mating, and egg laying have also occurred in German populations of blackcap warblers, *Sylvia atricapilla*. In the case of the mosquito *W. smithii*, these genetic shifts have been documented over as short a time span as five years (95, 97). Shifts in allozyme and chromosomal inversion frequencies that parallel climate change have been documented among four species of *Drosophila* on four continents. In the case of *Drosophila*, it is not yet clear whether the observed shifts in allozyme or inversion frequencies is due to the direct effects of hotter summers or to the indirect effects of a longer growing season in combination with a shorter winter (97). To date, a genetic shift in thermal tolerance or thermal optimum associated with recent rapid climate change has not been clearly demonstrated in any animal, although we have predicted that such a shift is likely to occur in *Drosophila* (97). The general pattern that has emerged is that recent rapid climate change is driving evolution (genetic change) at the level of the population and that the principal target of selection is the timing of seasonal events rather than thermal tolerance or thermal optima.

The evidence for evolutionary responses to recent rapid climate change is drawn almost exclusively from the level of population genetics. To date, there is only one QTL (quantitative trait loci) map for photoperiodic response in any animal (112), and no known genes segregating in natural populations that determine photoperiodic response have been identified in any animal.

CONCLUSIONS

Whereas the proximate effects of change in the nonbiological world are driven by the direct effects of temperature, the proximate effects of change in the biological world at temperate and polar latitudes are driven by response to changing seasons, orchestrated principally by light. The preeminence of light in the organization of the biological world at these latitudes is shown experimentally by the loss in fitness of more than 80% when incorrect day-length information is perceived; in contrast, fitness in the temperate zone actually improves in ectotherms experiencing warmer thermal conditions.

Physiological processes provide the functional connection between the genotype and the phenotype that ultimately confronts the environment and determines individual fitness. Organisms in nature encounter environmental variation and cope with that variation through physiological adjustments at the behavioral, hormonal, cellular, and biochemical levels. Many physiological functions respond directly to immediate environmental variation. Dealing with seasonal variation requires more elaborate physiological responses such as preparation for reproduction, dormancy, and migration. These more elaborate physiological responses require long preparatory periods, but future seasons are predictable from the annual change in day length. Animals from rotifers to rodents

use the length of day or photoperiodism to anticipate and prepare for future seasonal changes that provide opportunities for growth, development, and reproduction or that impose exigencies that can be mitigated or avoided through dormancy or migration.

Climate change is resulting in rapidly warming winters, slowly warming summers, earlier springs, later falls, and longer growing seasons. The direct effects of warming can be seen in the melting of glaciers and rising sea levels. However, animals are not glaciers, and at temperate and polar latitudes, climate warming is providing thermal opportunity, not exigency. The major target of selection is then on the physiological processes, principally photoperiodism, that animals use to time important events and seasonal transitions in their life histories. Animals with short life spans and rapid reproductive maturation usually respond to absolute day length; longer-lived animals with prolonged reproductive maturation usually rely on a combination of a direct response to absolute day length, the synchronization or setting of an internal circannual clock by increasing and decreasing day lengths, and a refractory period when animals are nonresponsive to day length.

In these cases, there is a light-initiated cascade of events from the input and interpretation of day length, through hormonal integration, to the output of specific hormones that determine whether animals prepare for and ultimately develop, reproduce, hibernate, diapause, or migrate. The go/no-go input and integration of light can occur months before or thousands of kilometers from the environment in which animals reproduce, migrate, or go dormant. Being at the right place at the right time is crucial to maintaining fitness at temperate and polar latitudes. Missing the right place at the right time results in reduced fitness and imposes selection on the population and, hence, the photoperiodic and hormonal processes that determine the timing of seasonal activities.

Over millennial timescales, seasonal selection along geographic climatic gradients has led to parallel patterns in genetic differences among populations in response to day length. Similarly, recent rapid climate change over tens of years in temperate and polar regions of the Earth has imposed seasonal selection over contemporary time. In response to this selection, animals from insects to birds and mammals have shown evolutionary changes (genetic shifts) in their seasonal activities over as short a timescale as five years. There is presently no clear case of a genetic shift toward higher thermal tolerance or thermal optima in any animal. Selection during recent rapid climate change in temperate and polar regions has principally affected seasonal timing, not thermal adaptation. Documentation of contemporary evolution and genetic change in animal populations has primarily been at the population genetic level, and although there is one QTL map for photoperiodic response, there are no genes segregating in natural populations that are known to contribute to the evolution of photoperiodic response. Molecular tools are now sufficiently developed so that they can be applied to a variety of nonmodel organisms. Investigators are therefore able to choose the organism best suited for determining the genetic basis of specific physiological processes identified as important for genetic adaptation to rapid climate change.

SUMMARY POINTS

1. Animals are not glaciers. The abiotic world responds directly to increasing temperatures as seen by warmer winters, earlier springs, later falls, longer growing seasons, rising sea levels, and melting glaciers. However, the biotic world has responded to recent rapid climate change by expanding ranges poleward and by altering the timing of important events in seasonal life histories, orchestrated principally by light.

2. Light (day length) should be seen as preeminent in temperate and polar regions in determining long-term fitness in animals unless experimentally shown otherwise. In a natural, yearlong study comparing light and temperature, insects lost 88% of fitness when given incorrect photic (light) information. However, fitness actually improved by more than 40% when the insects were given a warmer thermal environment. From a strictly thermal point of view, other investigators have shown that climate warming over the next century is expected to improve fitness of ectotherms at temperate and polar latitudes.
3. Timing is essential. Fitness at temperate and polar regions depends upon the ability to exploit the growing season, to avoid or mitigate the effects of winter, and to make a timely transition between the two lifestyles. Populations that are changing the timing of their seasonal activities are persisting; populations that have not changed or are changing slowly are in decline or going extinct.
4. Recent rapid climate change is already driving evolution in insects, birds, mammals, and plants. All documented cases of a genetic shift in populations related to recent climate change have involved altered timing of seasonal activities; there are no documented cases of increased thermal tolerance or increased thermal optimum.
5. The major physiological processes enabling temperate and polar animals to anticipate and prepare for their seasonal transitions involve the use of light. Animals use day length directly or in combination with circannual rhythmicity and a refractory period to arrive at the right place at the right time in their seasonal life cycles. As the optimal place and time change with climate, selection will be imposed on physiological timing mechanisms and the hormones that link those timing mechanisms with development, reproduction, migration, and dormancy.
6. Mechanism matters. Rather than assuming that a response to the direct effect of temperature is the primary target of selection during climate change, investigators should focus on altered photoperiodic and hormonal responses that enable animals to exploit opportunity and to mitigate exigencies in their seasonal environments.

FUTURE ISSUES

1. What are the genes responsible for genetic variation in response to day length within and between natural populations of animals? The ultimate discovery of the genes controlling photoperiodic response will be the foundation for understanding the evolutionary response by animals to rapid climate change in temperate and polar regions of the world.
2. What is the genetic relationship between the interpretation of day length (the photoperiodic timer) and the accumulation of day-length information (the photoperiodic counter) that leads to the triggering of downstream physiological cascades committing an animal to a go/no-go seasonal program?
3. What are the genetic connections integrating response to absolute day length, photoperiodic setting of the circannual clock, and the refractory period of animals from annelids to mammals? How do these three processes coevolve? Is their coevolution necessary for genetic response to rapid climate change, or are they free to evolve independently?

4. What is the pathway in birds between the input of light and the pars tuberalis? In mammals, what mechanisms distinguish between long and short days if both day lengths promote the same output of DIO2 to the median eminence of the hypothalamus?
5. Except for efforts to differentiate the importance of response to day length versus temperature throughout the year (*Ry*), the bulk of studies focus on the summer season. Yet, the winter season is the time of year when climate change is occurring the fastest. How will shorter and warmer winter temperatures affect physiological processes in animals such as chilling, energy balance, senescence, and aging?
6. As animals expand their ranges from the tropics to the temperate zone, how do they transition from dependency on tropical cues to day length to control their seasonal development? How fast is de novo evolution of response to day length?
7. In tropical regions, where day length plays little or no role in coordinating life-history responses, will the direct effects of temperature on thermal optima and thermal tolerance evolve, and what environmental cues will be used to predict seasonal changes in the tropics?
8. Can sufficient examples be garnered from existing data on rates of response to rapid climate change to infer patterns of survival of major taxa? How can these results be applied to effective conservation efforts?

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