Genetic response to rapid climate change: it's seasonal timing that matters

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Abstract

The primary nonbiological result of recent rapid climate change is warming winter temperatures, particularly at northern latitudes, leading to longer growing seasons and new seasonal exigencies and opportunities. Biological responses reflect selection due to the earlier arrival of spring, the later arrival of fall, or the increasing length of the growing season. Animals from rotifers to rodents use the high reliability of day length to time the seasonal transitions in their life histories that are crucial to fitness in temperate and polar environments: when to begin developing in the spring, when to reproduce, when to enter dormancy or when to migrate, thereby exploiting favourable temperatures and avoiding unfavourable temperatures. In documented cases of evolutionary (genetic) response to recent, rapid climate change, the role of day length (photoperiodism) ranges from causal to inhibitory; in no case has there been demonstrated a genetic shift in thermal optima or thermal tolerance. More effort should be made to explore the role of photoperiodism in genetic responses to climate change and to rule out the role of photoperiod in the timing of seasonal life histories before thermal adaptation is assumed to be the major evolutionary response to climate change.

Keywords: day length, evolution, genetic response, global warming, photoperiodism, seasonal timing

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Introduction

The major effect of climate warming on biotic (biological) systems results from increasing the length of the growing season and altering the optimal time for life-history transitions such as development, reproduction, dormancy and migration. Genetic changes in animal populations (evolution) reflect selection due to earlier springs, later falls and increasing length of the growing season, resulting in earlier arrival and reproduction, later dormancy and an increase in the frequency of summer genotypes (Bradshaw & Holzapfel 2006). In no case has there been shown a genetic change in thermal optima or heat tolerance associated with recent rapid climate warming in animals. This observation is not surprising. In nature, clear patterns of evolved differences in thermal responses occur primarily among species or genera (Brattstrom 1968; Parsons 1981; Hochachka & Somero 1984;

van Berkum 1986, 1988; Huey & Bennett 1987; Gibert *et al.* 2001), and are usually weak or absent among populations within species occupying even a broad climatic range (Hertz *et al.* 1983; Crowley 1985; Delpuech *et al.* 1995; Tauber *et al.* 1987; van Berkum 1988; Lynch 1992; but see Dahlgaard *et al.* 2001; Hoffmann *et al.* 2001, 2002). By contrast, photoperiodic response varies widely within species of insects, amphibians, birds and mammals and is closely associated with climate (Bradshaw & Holzapfel 2007). Within insects that show geographical variation in both thermal and photoperiodic response, that of photoperiodic response tracks the climatic gradient more closely (Kimura 1984, 1988; Hawley *et al.* 1987; Fochs *et al.* 1994; Hanson & Craig 1994, 1995; Hanson 1995; Bradshaw *et al.* 2004). The latitudinal gradient in climate is due more to winter cold than summer heat (Fig. 1) and among temperate ectotherms, upper thermal limits generally vary less over latitudinal gradients than do lower thermal limits (Zani *et al.* 2005). Consequently, we expect successful adaptation to recent, rapid climate change to involve primarily genetic shifts in photoperiodic response rather than thermal tolerance or thermal optima.

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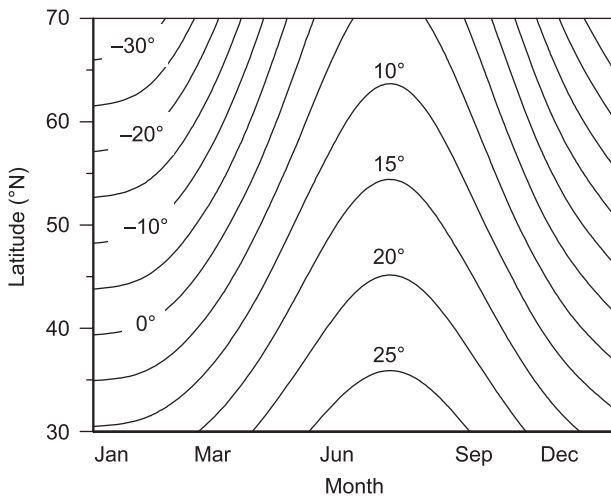E-mail: mosquito@uoregon.edu

Fig. 1 Geographical and seasonal variation in temperature in central and eastern North America. Isotherms show mean monthly temperatures (°C). The latitudinal variation in climate is less a matter of summer warmth (June isotherms are far apart) than it is of winter cold (January isotherms are close together) and northern populations experience a shorter growing season than do southern populations. Recent rapid climate change is having a greater effect on winter cold than on summer heat. The result is milder winters, longer summers, earlier springs and later onset of winters. Climate warming is ameliorating winter cold without imposing an appreciable increase in summer heat and thus is extending the growing season; these effects increase with latitude, effectively shifting the isotherms upwards. Hence, the increasing length of the growing season and the advance and delay of spring and winter, respectively, impose greater selection on animal populations than does the direct effect of temperature. Data for 34 localities were collated from 30 to 49°N (ESSA 1968) and from 50 to 70°N (Environment Canada http://www.msc.ec.gc.ca/climate/climate_normals_1990/show_normals_e.cfm) and subjected to nonlinear regression ($R^2 = 0.95$): °C = 47.10−0.87(°latitude) − 5.96(km altitude) + 1.175 Cos[(month − 12.18)∗π/6.01].

Effects of climate warming on animals

The popular conception is that current rapid climate warming means an increase in summer heat, which, in turn, selects for increased thermal tolerance. However, at temperate and higher latitudes the major effect of global warming is, in fact, on winter cold, not summer heat, and this effect becomes greater as one moves pole ward (IPCC 2001, 2007). Global warming makes temperate and polar climates more like equatorial climates: it reduces the duration and severity of winter cold without substantially increasing summer heat. As a consequence of winter warming at temperate and arctic regions, spring arrives earlier and winter arrives later, resulting in an earlier or longer season favourable for growth, development and reproduction. Hence, northern latitudes are becoming more like southern latitudes, effectively moving the iso-

therms in Fig. 1 upwards. The net effect is to alleviate the effects of winter cold without appreciably increasing summer heat while imposing selection for altered timing of events in the seasonal life histories of animals (Bradshaw *et al.* 2004).

How animals regulate the timing of seasonal activities

The principal means by which temperate and polar animals from rotifers to rodents regulate the timing of major seasonal events is by using the length of day or photoperiod (Box 1). By using day length, animals are able to maximize opportunities during the favourable season and to minimize exposure or the consequences of exposure to deleterious or otherwise lethal temperatures. Rather than confronting the adverse effects of climate warming directly, many animals are avoiding or mitigating these adversities by developing and reproducing at times of the year when they do not occur. Animals are able to do so both through phenotypic plasticity and through rapidly evolving genetic shifts in the programming of their seasonal life histories. Since day length is the principal cue used to program seasonal activities in arthropods (Danilevskii 1965; Danks 1987), teleost fish (Bromage *et al.* 2001), birds (Dawson *et al.* 2001; Dawson 2002; Coppack & Pulido 2004) and mammals (Hofman 2004; Goldman 2001), the immediate genetic adaptations of these animals to climate change should involve the physiological mechanisms related to photoperiodic response and not to the physiological mechanisms used to confront seasonal stress directly (Bradshaw & Holzapfel 2001a, 2006; Bradshaw *et al.* 2004). Current examples of genetic response to climate change in animals include genetic shifts in photoperiodic response directly, genetic increase in the ability to use temperature as an anticipatory cue when photoperiodic response remains genetically inflexible, genetic change in migration direction facilitated by phenotypic plasticity in photoperiodic response, and implied genetic shifts in photoperiodically cued timing of migration and reproduction.

Response of animals to recent rapid climate change

The phenotypic 'signature' of biotic response to climate change is seen primarily in the northward expansion of species' ranges, the earlier migration and reproduction in the spring, and the later migration or entrance into hibernation in the fall (Hughes 2000; Peñuelas & Filella 2001; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Warren 2006). Below we review the clearest examples we could find in which genetic change due to climate warming has been documented. The mechanism of response to climate change is specific to each case but all of them involve genetic changes related to seasonality;

Box 1 Generalizations about photoperiodism in animals (Bradshaw & Holzapfel 2007); Box 2 provides a brief glossary of terms

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, fresh water, and terrestrial habitats use the length of day (photoperiodism) to anticipate and prepare for seasonal transitions of major events in their life histories,

1 Unlike temperature or rainfall, the annual change in day length at any location is invariant from year to year. Day length therefore provides a highly reliable anticipatory cue for future 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 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.

none involves a genetic increase in thermal optimum or in heat tolerance. We note that although we could not find any explicit test for a genetic shift in thermal optimum or heat tolerance attributable to climate change, we did find a widespread assumption that such adaptation must be happening. Selection on thermal tolerance or thermal optima by climate change appears to be a hypothesis accepted because of its inherent plausibility rather than because of the results of explicit experimental tests.

The North American mosquito, Wyeomyia smithii

Wyeomyia smithii lays its eggs and completes its pre-adult development only within the water-filled leaves of the purple pitcher plant, *Sarracenia purpurea*. The range of the mosquito follows that of its host plant from the Gulf of Mexico to northern Canada. Throughout this range, *W. smithii* enter a larval diapause whose onset, maintenance and termination are mediated by photoperiod. The day length that switches larvae from continuous development to dormancy (diapause) or stimulates the resumption of development (the critical photoperiod) increases with latitude and altitude, so that larvae enter diapause earlier in the year at higher latitudes or altitudes where winters arrive earlier when days are longer than in the south or lowland localities (Bradshaw & Lounibos 1977).

We used *W. smithii* to determine the relative selective importance of temperature vs. photoperiodism during rapid climate warming (Bradshaw *et al.* 2004). Using computer-driven, controlled-environment rooms, we simulated the natural, annual progression of temperatures and day lengths of a northern (Newfoundland) and a southern (New Jersey) climate. We then 'transplanted' replicate northern populations to the southern climate, representing a climate change equivalent to 180–200 years of global warming at its present rate, and maintained controls in their native northern climate. We determined fitness as the year-long cohort replacement rate, integrating performance over all four seasons. The experiment pertinent to climate change involved three treatments:

1 Populations from northern latitudes were exposed to a northern climate with fixed day lengths that enabled them to enter and then terminate diapause at the appropriate time of year for the northern latitude.
2 Populations from northern latitudes were exposed to a southern climate with fixed day lengths that enabled them to enter and then terminate diapause at the appropriate time of year for the southern latitude.
3 Populations from northern latitudes were exposed to the same southern climate as in treatment 2 but with the naturally changing day lengths of the southern latitude.

Box 2 Glossary

Adaptation: genetic change in a population due to natural selection, leading to improvement of some function or increased suitability to some aspect of its environment.

Circannual rhythms: internal (endogenous) physiological rhythms with a period of about a year; circannual rhythms are most often 'set' by photoperiod.

Critical photoperiod: the length of day that induces a 50% long-day and 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, and vice versa.

Diapause: arthropod dormancy, may be hibernal or aestival.

Heritability: strictly, the ratio of additive to phenotypic variance; colloquially, the amount of genetic variation that is exposed to selection; a measure of the efficiency of response to selection.

Parturition: giving birth.

Phenology: the annual timing of life-history events in a population.

Phenotypic plasticity: the ability of an individual to develop any of several phenotypes, depending on the environment.

Photoperiodism: the ability to assess the length of day or night to regulate behaviour, physiology, development or reproduction.

Refractory: inability to respond to day length; herein, the 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 temperature.

Populations in treatment 2 achieved a threefold increase in fitness relative to treatment 1. Hence, when the differences in genetically programmed responses to day length were experimentally factored out, the milder southern climate was thermally benign compared to the native northern climate. Thermally, climate warming should alleviate, not exacerbate thermal stress on these populations. Populations in treatment 3 lost 88% of fitness compared to treatment 2. Hence, in a benign thermal climate, fitness was critically dependent upon possessing the correct, genetically determined response to day length. Simply put, imposing the thermal pattern of 180–200 years of climate warming actually resulted in increased fitness among northern populations, but when these same populations encounter the wrong day length, they lose 88% of fitness.

Since the annual change in day length varies with latitude (Fig. 2) and for reasons we explain above, transplants from northern to southern localities in nature cannot be used to evaluate the potential impact of climate warming because the effects of the novel photic environment will always compound or occlude the effects of temperature or drought. However, the effects of changing thermal or moisture environments can correctly be made by transplants across longitudes (e.g. Fenster & Galloway 2000), between altitudes at the same latitude as in the historic experiments of Clausen *et al*. (1940) or across time at the same locality by comparing contemporary with ancestral plants resurrected from appropriately stored seed (e.g. Franks *et al*. 2007).

Genetic correlations can either impede or facilitate response to selection. In *W. smithii*, generation time and critical photoperiod are positively genetically correlated (Hard *et al*. 1993), i.e. animals with shorter generation times are genetically predisposed to enter dormancy later in the year, in accord with theoretical predictions (Istock *et al*. 1976; Taylor 1980). Hence, selection for shorter, more southern critical photoperiods due to longer growing seasons is facilitated by correlated selection for shorter generations.

The heritability (h^2 = efficiency of response to selection) of critical photoperiod increases with latitude (Bradshaw & Holzapfel 2001b), as does the rate of climate change (IPCC 2001, 2007). Over the last 30 years, there has been a genetic shift towards shorter, more southern critical photoperiods and this shift is detectable over as short a time span as five years (Bradshaw & Holzapfel 2001a). Since the response to selection, R = h^2S, is the product of the heritability (h^2) of the trait under selection and the strength of selection (S = rate of climate change) applied to that trait, it is no surprise that the shift has increased with latitude (Bradshaw & Holzapfel 2001a). Hence, with increasing extension of the growing season into the fall, *W. smithii* have evolved later entry into diapause.

The European blackcap, Sylvia atricapilla

Reproductive success among insectivorous birds is dependent upon concordant timing of food availability and chicks in the nest. With increasing climate warming, there is a mismatch between photoperiodically timed egg-laying in homeothermic birds and the temperature-driven development of their ectothermic prey during the spring. By the time birds have chicks in the nests,
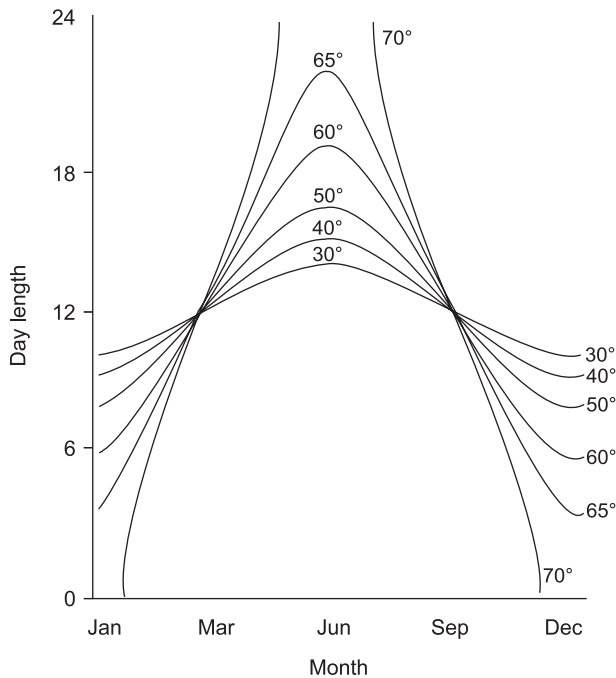
Fig. 2 Geographical and seasonal variation in day length (sunrise to sunset) over the same latitudinal range as in Fig. 1. The annual change in day length increases with latitude and is unaffected by climate warming: at any latitude, the day length is the same today as it was on this date 10 or 10 000 years ago. Consequently, day length at temperate and polar latitudes predicts future seasons more reliably than any other environmental cue. Note that transplanting a plant or animal with a threshold day length or critical photoperiod of 18 h of light per day from 60 to 50°N places that organism in a photic environment where it will never see a long day, leading to the omission or mistiming of development, reproduction, dormancy or migration. Hence, fitness in temperate and polar latitudes is critically dependent on concordance between the external seasonal environment (Fig. 1) and the internal, genetically determined response to day length. Redrawn from Danilevskii (1965).

caterpillar prey have metamorphosed and are no longer available. Hence, there is, in general, selection for earlier reproduction in the spring (Visser *et al.* 2004).

A population of the blackcaps in southern Germany has historically migrated to and spent the winter in Iberia, but over the last 30 years, an increasing proportion of this population is now overwintering in Britain (Terrill & Berthold 1990; Bearhop *et al.* 2005). British birds begin to migrate back to Germany earlier than Iberian birds, have a shorter migratory distance to cover and arrive at the nesting areas earlier than the Iberian birds. Early-arriving males are able to defend the best territories and early-arriving females consort with males that have the best territories and realize greater reproductive success than late-arriving birds (Terrill & Berthold 1990). This assortative mating reinforces the increasing tendency of birds to

overwinter in Britain. Two factors enable this rapid change in the timing of blackcap reproduction. First, there is a genetic shift in the direction of autumnal migration from southwest (towards Iberia) to due west (towards Britain) (Berthold *et al.* 1992). Second, birds exposed to British winter photoperiods initiate migration earlier than birds exposed to Iberian winter photoperiods (Terrill & Berthold 1990). The earlier migration of British birds may involve little or no genetic change in photoperiodic response. At the end of the nesting season, long days terminate reproductive behaviour, initiate moulting, and render birds refractory to long-day stimulation of gonadogenesis. This refractory state is generally terminated by exposure to short days. Termination of refractoriness proceeds faster at shorter than longer winter day lengths (Coppack *et al.* 2003). Midwinter day lengths are shorter at more northern latitudes (Britain) than at more southern latitudes (Spain). Hence, birds overwintering in Britain terminate refractoriness earlier than those in Spain and are able to respond more immediately to the increasing day lengths of spring (Terrill & Berthold 1990). The ability of the blackcap to keep pace with advancing spring has therefore been due to a genetic shift in migratory orientation at the population level, facilitated by a phenotypically plastic response to winter day lengths by individual birds.

In addition to selecting for early arrival at the breeding grounds, climate warming should also select for decreased migratoriness, shorter migration distances, weaker migratory tendencies and later departure from the breeding grounds (Pulido & Berthold 2003). The amount and intensity of migratory activity are positively genetically correlated and, together, are negatively genetically correlated with the timing of migratory onset in the fall. Later migrating birds are genetically predisposed to weaker migratory intensity and shorter migratory distances. Hence, the evolution of later autumnal migration should be reinforced by these genetic correlations. However, earlier nesting in the spring exposes juveniles to (i) increasing day lengths of spring and then long days of summer rather than (ii) just the long days of summer. This exposure advances the onset and increases the duration of both the post-juvenile molt and nocturnal migratory activity (Coppack *et al.* 2001). This apparently maladaptive response to day length is counterbalanced by the higher annual survivorship of the British relative to the Iberian migrants due to supplemental feeding and decreased migration distance as well as enhanced reproductive success of early breeding birds (Terrill & Berthold 1990). The net result should be a continuation of early migration coupled with rapid evolutionary response of the photoperiodic timing of the post-juvenile molt and onset of migration due to the high heritability of photoperiodic response and the underlying genetic correlation structure.

The Yukon red squirrel, Tamiascurus hudsonicus

Drought stress induced by recent climate warming in northwest Canada has led to increased spruce cone production, leading to earlier breeding by squirrels in subsequent years. In addition, earlier springs allow females to enter a positive energy balance earlier in the year, permitting them to develop litters sooner (Réale *et al.* 2003a, b). Pedigree analysis using the 'animal model' shows that the heritability of parturition date is $h^2 = 0.15$ and that about 13% of the 18-day advance in mean parturition date over a 10-year period is genetic (Réale *et al.* 2003a, b). The basis of this genetic response is not known but photoperiodism is the strongest synchronizer of seasonal events in the life cycle of most mammals (Hofman 2004) and, at least in mice, the incidence of photoperiodically mediated gonadal regression increases with latitude (Sullivan & Lynch 1986; Heideman *et al.* 1999). We therefore suspect that photoperiodism plays a role in the seasonal timing of parturition of *Tamiascurus hudsonicus*, either directly or indirectly through setting of the circannual clock (Goldman 2001).

The European great tit, Parus major

Date of egg laying in a Dutch population of great tits has not advanced over a 23-year period, despite intensifying directional selection for early egg-laying (Visser *et al.* 1998). Great tits rely upon caterpillars feeding on buds in an oak forest to feed their chicks. Due to earlier bud burst, peak caterpillar abundance has advanced 20 days while egg-laying day has not advanced and late-reproducing birds suffer greatly reduced reproductive success.

Great tits are photoperiodic and the threshold day length for stimulating gonadal maturation increases with latitude. However, a Swedish population initiated 50 years ago from a southern population has a shorter threshold day length than would be expected for its latitude (Silverin *et al.* 1993). It would therefore appear that photoperiodic response in great tits has a low heritability and would explain the inability of the Dutch population to advance the timing of their egg-laying with advancing caterpillar abundance.

Part of the mismatch is compensated for by a trend towards a reduced time interval between laying of the first egg and hatching (Visser *et al.* 1998) and part through heritable phenotypic plasticity in response to temperature. The great tit population is polymorphic for birds able to use temperature as an environmental cue to advance egg-laying in warm years and delay egg-laying in cool years (Nussey *et al.* 2005). These phenotypically plastic females show increased synchrony between egg-laying and caterpillar abundance, have more resources for provisioning their chicks and have more of their offspring recruit into the population as breeding adults.

The important point illustrated by the great tits is that in lieu of a genetic shift in photoperiodic response, there is a genetic shift towards increased phenotypic plasticity in egg-laying date. Genetically flexible females are able to use spring temperature as an environmental signal to modify egg-laying date in earlier or later springs. However, the rate of increase in the population as a whole of females able to track the vernal environment of individual years is not keeping pace with the rate of climate warming and the population's viability may ultimately be threatened (Nussey *et al.* 2005). Genetic inflexibility of photoperiodic response is impeding genetic adaptation to earlier springs in the great tit.

The European barn swallow, Hirundo rustica

Barn swallows nest in Denmark but overwinter in southern Africa and have a high heritability for arrival date at nesting localities. Over the last 33 years, birds have arrived progressively earlier and early arrival increases reproductive success in both sexes equally. However, there has been an advance in male but not female arrival date, resulting in increased protandry due to differences in viability selection on each sex by earlier springs. Phenotypic plasticity in arrival date estimated as the difference in arrival date of the same individual in successive years did not change during the study (Møller 2007).

The timing of long-distance migrants like barn swallows is likely determined by an endogenous circannual rhythm that is set by day length (Gwinner 1996). The high heritability and absence of phenotypic plasticity indicate that the advance timing of vernal arrival over the last 33 years of climate change has been due to genetic modification of the day lengths used to set the circannual clock or of the circannual clock itself.

Fruit flies, Drosophila

Dobzhansky (1948) observed that chromosomal inversions in Californian populations of *Drosophila pseudoobscura* changed with seasonality such that the frequency of certain inversions increased during the summer and decreased during the winter. At the same time, the frequency of the winter inversions increased with latitude and altitude. Hence, the inversions are under seasonal selection.

Seasonal cycling and a latitudinal cline in inversion frequencies also occur in European *Drosophila subobscura*. With increased climate warming the frequency of the northern inversion declined over 16 years in Spanish populations (Rodríguez-Trelles & Rodríguez 1998). During the 1970s, *D. subobscura* has also independently invaded western North and South America and on both continents established a latitudinal cline in inversion frequencies reflecting the ancestral cline in Europe (Prevosti *et al.* 1988;

Ayala *et al*. 1989). After 24 years between samplings, climates had warmed significantly in 22 of 26 populations and, concomitantly, in 21 of these populations, there has been a shift towards inversions characteristic of low latitudes on all three continents (Balanyá *et al*. 2006). In central and eastern North America, there has also been an increasing frequency of southern inversions in *Drosophila robusta* that parallels increasing local minimum air temperatures (Levitan 2003; Levitan & Etges 2005). Finally, over a 20-year period in eastern Australia, there has been a northern shift in both inversion and allozyme frequencies in populations of *Drosophila melanogaster* (Umina *et al*. 2005). Hence, at the local, continental, and global scales, there has been a shift towards equatiorial or low-altitude inversions or allozyme frequencies that parallels recent climate warming across four species of *Drosophila* and four continents.

The increase in the 'summer' or 'equatiorial' inversions means that in populations as a whole, there has been a genetic shift towards genotypes associated with warmer climate. However, it is not known whether this genetic shift has been due to hotter summer temperatures, per se, or due to a longer warm and a shorter cool season during which the alternative selective forces can act. In the first case, we would expect there to be greater thermal tolerance or a higher thermal optimum for the summer or winter inversions in contemporary than ancestral populations. In the second case, we would expect there to be no change in thermal tolerance or optima associated with specific inversions and would conclude that the shift in inversion frequency has been due to the length of the growing season rather than higher temperatures, per se. In addition, there is a latitudinal cline in genetic tendency to diapause among populations of *D. melanogaster* (Schmidt *et al*. 2005; Tauber *et al*. 2007) and a Dutch population of *D. melanogaster* has a longer critical photoperiod than Italian populations (Tauber *et al*. 2007). The changes in inversion frequencies may therefore also be related to selection for reduced incidence of diapause or a shorter critical photoperiod. In short, we know that southern inversion and allozyme frequencies are positively correlated with recent, rapid climate change but not whether this pattern results from selection on thermal optima, thermal tolerance, season length, incidence of diapause or photoperiodic response. Nonetheless, we believe that *Drosophila*, with its short generation time and large population size may hold the greatest promise for demonstrating genetic shifts in thermal tolerance or thermal optima in response to rapid climate change.

Limits to biotic responses to climate change

Initially, animals cope with altered seasonal environments by specific responses of individual organisms (phenotypic plasticity). Each individual in a population has a preset phenotypic repertoire; some individuals can accommodate large environmental variations; other individuals can tolerate only a narrow range of environmental variation. As climate warming continues, shifting optima for the timing of development, reproduction, migration and dormancy will exceed the limits of individual plasticity and selection for genetic change in populations will occur. Ultimately, the ability of animal populations to persist will depend upon the sources of standing genetic variation within populations and additional variation generated by mutation and immigration (Lynch 1996; Bijlsma *et al*. 1997; Bürger & Lynch 1997; Berteaux *et al*. 2004). In animal populations, response to climate change has involved both phenotypic plasticity and genetic change (evolution) and has involved some aspect of seasonality. Among animals that do show actual genetic change, photoperiodism: (i) can be a direct causal mechanism of genetic change (mosquito); (ii) can facilitate a genetic change due to its phenotypic plasticity (blackcap); (iii) can impede adaptation due to its genetic inflexibility (great tit); (iv) is a likely mechanism of genetic change (squirrel, barn swallow); and (v) is a possible mechanism of genetic change (*Drosophila*).

Given the pervasiveness of photoperiodism in rotifers, annelids, arthropods, echinoderms, teleost fish, amphibians, lizards, birds and mammals (Bradshaw & Holzapfel 2007), we conclude that more effort should be made to explore the role of photoperiodism in the animals currently exhibiting genetic responses to climate change and to rule out the role of photoperiod in the timing of seasonal life histories before the direct effects of temperature are assumed to be the mechanism underlying evolutionary response to climate change.

Implications

1 None of the evolutionary (genetic) responses we discuss, nor any to our knowledge, show an increase in heat tolerance or in thermal optima in response to recent, rapid climate change. We therefore propose that the emphasis placed on the direct effects of summer temperature on organisms is misdirected. Rather, it is the *indirect* effects of climate warming on the advancement of spring, on longer growing seasons, and on the delayed onset of winter that are imposing selection on animal populations. For most cases, it will be the efficiency of response to selection on photoperiodism or phenotypic plasticity in photoperiodic response that will determine the ability of populations to persist in place or to expand their ranges northwards into novel photic environments.

2 The climate is warming and will continue to do so (IPCC 2007). Because winters are warming faster than summers, warming of temperate and polar populations results in the amelioration of winter cold stress

without imposing appreciable summer heat stress. The northward extension of animal populations is well documented; whether those expanding populations are displacing local species or whether the southern borders of species distributions are receding is less well documented. Such documentation is crucial for determining whether climate warming is leading to an increase or decrease in biodiversity of temperate and northern latitudes. Many species, especially large animals with long generation times and small population sizes already at the altitudinal or latitudinal limits of their range likely face extinction; but, the question remains whether the loss of diversity by their extinction will be replaced by northward migrants.

3 Questions we need to answer: What other animal species have changed genetically in photoperiodic response as a result of recent rapid climate change? Are there examples of genetic change within species in thermal optima or heat tolerance as a result of recent rapid climate change? What are the genetic bases of photoperiodism and seasonal adaptations? What are the limits of phenotypic plasticity and genetic abilities of animal populations to keep pace with advancing springs, longer growing seasons and later onset of winters? How can we prepare for the inevitable advances into higher latitudes of the zones for agricultural crops, of the zones in which tropical diseases of wildlife, humans and livestock are transmitted, and in the conditions under which we maintain managed populations?

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William E. Bradshaw and Christina M. Holzapfel work together on the genetics, evolution, physiology and ecology of climatic adaptation, particularly in the pitcher-plant mosquito, *Wyeomyia smithii*. Currently, they are involved in determining the relationship between the circadian clock and photoperiodism, the relative rates of thermal and photoperiodic adaptation to climate warming, and molecular mechanisms of photoperiodic time measurement using real-time qPCR, QTL mapping and microarrays in collaboration with their graduate students, Kevin Emerson and Derrick Mathias and with Charalambos Kyriacou, Ezio Rosato and Eran Tauber at the University of Leicester, UK. They have also entered into collaboration with William Cresko at the University of Oregon and Paul Schmidt at the University of Pennsylvania working on the genetics and evolution of photoperiodism in stickleback fish and *Drosophila melanogaster*, respectively.