Photoperiodic Response and the Adaptability of Avian Life Cycles to Environmental Change

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I. SUMMARY

In birds, the annual change in daylength is the most important environmental cue used for synchronising breeding, moult, and migration with recurrent seasonal fluctuation in environmental conditions. Human-caused environmental changes may affect photo-responsive birds in two ways: (1) The photoperiod may become an unreliable predictor of favourable conditions if the phase relationship between temperature-dependent resource availability and daylength changes. For example, advances in the timing of breeding in response to increased spring temperature expose juvenile birds to altered photoperiodic conditions, which may result in unseasonably early autumn migration. (2) Range shifts and expansions may expose birds to novel photoperiodic conditions. Extant responses to these conditions could limit the potential of birds to evade increasingly unsuitable habitats and to establish new breeding and wintering

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grounds. However, if birds respond to novel photoperiodic conditions in an adaptive way—i.e., the elicited phenotypic change is in accord with the direction of selection—then adaptation of avian life cycles to global environmental change will be facilitated. In the course of environmental change, we expect the photoperiodic response itself to be the target of selection. However, adaptive evolution of the response to daylength may not keep pace with rapid environmental changes because of unfavourable genetic correlations among life-cycle stages or the lack of within-population genetic variation in phenotypic plasticity.

II. INTRODUCTION

A. General Introduction

The Earth's atmosphere is currently warming at an unprecedented rate (see "Preface"). This is expected—and has been shown—to have profound ecological and evolutionary consequences (McCarty, 2001; Walther *et al.*, 2002). The best documented biological response to recent climatic change is the change in the timing of seasonal events in plants, insects, and birds (Parmesan and Yohe, 2003; Root *et al.*, 2003). Changes in ambient temperature may affect animal and plant phenology directly or may have indirect effects by changing the environment in which selection occurs, i.e., by altering the availability of food resources and the prevalence of predators, parasites, competitors, and mates. Species that rely on the annual change in daylength for timing their life cycles, like most birds, will become desynchronised with the temperature-dependent selective environment, if photoperiodic responses do not change correspondingly (Visser *et al.*, 1998, 2004, this volume; Visser and Holleman, 2001).

A dramatic rise in global temperature will not only alter the timing of seasons but also the geographic location of suitable habitats, which, in turn, will have an impact on the distribution of animal and plant species—in particular highly mobile organisms, like birds (Root, 1993; Thomas and Lennon, 1999). Whether range shifts and colonisation of new habitats are possible hinges upon the ability of species and populations to appropriately respond to novel photoperiodic conditions. If the new conditions have rarely or never been encountered before in the evolutionary history of the population, adaptive reaction norms may not exist. *De novo* evolution of phenotypic plasticity and the evolvability of reaction norms may be constrained by the lack of genetic variation or by unfavourable genetic correlations with other life-history traits. Alternatively, if global environmental changes have recurrently been experienced, birds may have evolved highly adjustable photoperiodic response systems that adapt them to a wide range of environmental conditions.

The aim of this chapter is to give an overview of the consequences of photoperiodic responsiveness for the adaptability of birds to human-caused environmental change. It will focus on the question to what extent photoperiodic responses facilitate or constrain the adaptation of avian life cycles to novel environmental conditions.

B. Photoperiodic Control of Avian Seasonality

Birds match their reproduction with periods of highest resource availability (Lack, 1968; Perrins, 1970). The ultimate cause for this close synchronisation between breeding and the peak in food abundance is the high resource demand during chick-rearing (e.g., Daan *et al.*, 1988; van Noordwijk *et al.*, 1995; Nager *et al.*, 1997; Thomas *et al.*, 2001). In contrast to mammals, most birds are not capable of storing nutrients for raising their young and depend on specific protein-rich food resources, which are often only available during a short period. In principle, food abundance itself could function as the positive stimulus for initiating egg laying (Daan *et al.*, 1988; Nager *et al.*, 1997). However, in seasonal environments, initial predictive cues (*sensu* Wingfield, 1980) are required for initiating spring migration and gonadal development well in advance of favourable breeding conditions.

The seasonal change in daylength provides the most reliable source of temporal information about the environment and has been adopted by birds in the course of evolution as the main environmental cue for synchronising reproduction, moult, and migration with favourable environmental conditions. Other factors, such as temperature, rainfall, food abundance, and social stimuli may also affect the timing of life-cycle stages, but provide only short-term predictive information. These factors serve as supplementary cues for fine-tuning the rate of gonadal growth and the timing of breeding with local phenological conditions (see reviews by Wingfield *et al.*, 1992, 1993; Hahn *et al.*, 1997; Visser and Lambrechts, 1999).

Many empirical studies have explored the role of daylength in the control of avian seasonality (for reviews see Dawson *et al.*, 2001; Dawson, 2002). Most studies have been carried out with resident or short-distance migratory species of the temperate zone. Outside the tropics, the time of year is immediately apparent from the regular sinusoidal change in daylength, and all species experiencing these conditions appear to be photoperiodic. Birds living in tropical regions, in contrast, experience only slight changes in photoperiod and have been considered to be unable to use daylength as a cue for controlling seasonality (e.g., Dittami and Gwinner, 1985). However, recent evidence suggests that even

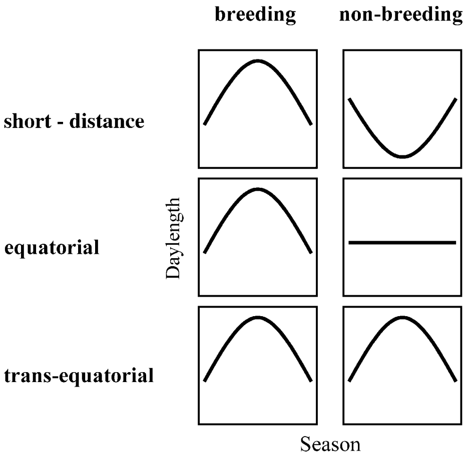

Figure 1 Photoperiodic conditions experienced on the breeding and non-breeding grounds by different types of migrants (schematic).

tropical species have evolved (or retained) the ability to respond to photoperiodic change (Hau, 2001; Styrsky *et al.*, 2004).

In migratory songbirds, which encounter complex photoperiodic conditions throughout the year (Figure 1), daylength acts as a synchroniser (*Zeitgeber*), entraining endogenous circannual rhythms of gonadal maturation, moult, and nocturnal migratory activity (Gwinner, 1986, 1996a,b; Berthold, 1996). With regard to the photoperiodic response, the annual cycle of a migratory bird can be divided into two phases in which short and long days exert different effects on the timing of life-cycle events (cf., Gwinner, 1996b).

During the post-breeding phase, from summer to late autumn, the onset of juvenile/post-breeding moult is advanced and its duration reduced by short photoperiods. Consequently, autumn migratory activity is initiated at an earlier age. This accelerated transition of life-cycle stages is supposed to be adaptive in that it enables birds hatching or breeding late in the season to moult and initiate migration before conditions deteriorate on the breeding grounds (Berthold, 1996). Long days after breeding induce gonadal regression and reproductive photorefractoriness, i.e., insensitivity of the hypothalamus–pituitary–gonadal axes towards long-day stimulation (reviewed by Hahn *et al.*, 1997; Nicholls *et al.*, 1988; Dawson *et al.*, 2001). Sexual immaturity after hatching may be caused by an innate photorefractory state, similar to photorefractoriness in adult birds, and exposure to short days generally promotes the termination of photorefractoriness. In the European starling (*Sturnus vulgaris*), juvenile photorefractoriness is terminated by short photoperiods, and premature exposure to short days leads to early gonadal development (Williams *et al.*, 1987). In the garden warbler (*Sylvia borin*)—a Palaearctic long-distance migrant that winters in central and southern Africa (Moreau, 1972)—termination of photorefractoriness and the post-refractory increase in photosensitive is predominantly controlled by endogenous factors (Gwinner *et al.*, 1988), but is possibly also modified by daylength conditions.

In the prenuptial phase, i.e., from winter through spring, the initiation of spring migration and gonadal growth are advanced by long (or increasing) daylengths (e.g., Rowan, 1925; for an example of such a response in a non-passerine migrant, see Rees, 1982, 1989). Also in long-distance migratory species wintering close to the Equator or beyond it (e.g., garden warbler, spotted flycatcher, *Muscicapa striata*), spring departure from the wintering site may strongly depend on photoperiodic conditions (e.g., Gwinner, 1987; Kok *et al.*, 1991). Experimental data suggest that garden warblers overwintering south of the Equator—where they experience longer daylengths than conspecifics wintering further north—advance prenuptial moult, gonadal growth, and the onset of spring migratory activity in response to the photoperiodic environment (Gwinner, 1987). It is supposed that this advancement of spring migratory disposition is adaptive in that it enables individuals wintering far south to reach their northern breeding grounds in time, in spite of the longer distance they have to travel (Gwinner, 1987, 1996a).

An additional point must be made about the significance of photoperiodic responses for birds breeding (or hatching) at very high latitude, i.e., under continuous light. Experimental data on captive bluethroats (*Luscinia svecica*) breeding at 66°N latitude show that the timing of post-breeding moult is inflexible against photoperiodically imposed time stress and suggest that the timing of moult is set early in the season and is endogenously determined (Lindström *et al.*, 1994). However, experiments by Pohl (1999) imply that passerine birds breeding in high Arctic regions may well use daily changes in the spectral composition of sunlight as a cue for synchronising physiological and behavioural rhythms, if periodic changes in light intensity are unperceivable.

C. Photoperiodic Response and Environmental Change

Climate change has been shown to cause a decoupling of phenological relationships between predators and their prey (Buse *et al.*, 1999; Visser and Holleman, 2001; Stenseth and Mysterud, 2002). For example, the timing of the great tit's (*Parus major*) breeding season in the Netherlands has remained unaffected by increasing spring temperatures, even though the date of highest caterpillar abundance has become earlier and selection for earlier breeding has intensified (Visser *et al.*, 1998). In this population, an adaptive advancement of breeding has not occurred, most likely because the cues used for initiating reproduction have not changed with the advancement of spring (Visser *et al.*, 1998). It is likely that this mismatch between resource availability and demand is in part the result the species' rigid photoperiodic control system. Great tits depend strongly on photoperiodic stimuli for initiating gonadal growth (Silverin, 1994), and intraspecific variation in egg-laying date is attributable to among-population differences in photoresponsiveness (Figure 2; Silverin *et al.*, 1993). Similarly, differences in the timing of breeding between blue tit (*P. caeruleus*) populations adapted to different seasonal environments (southern France versus Corsica) are

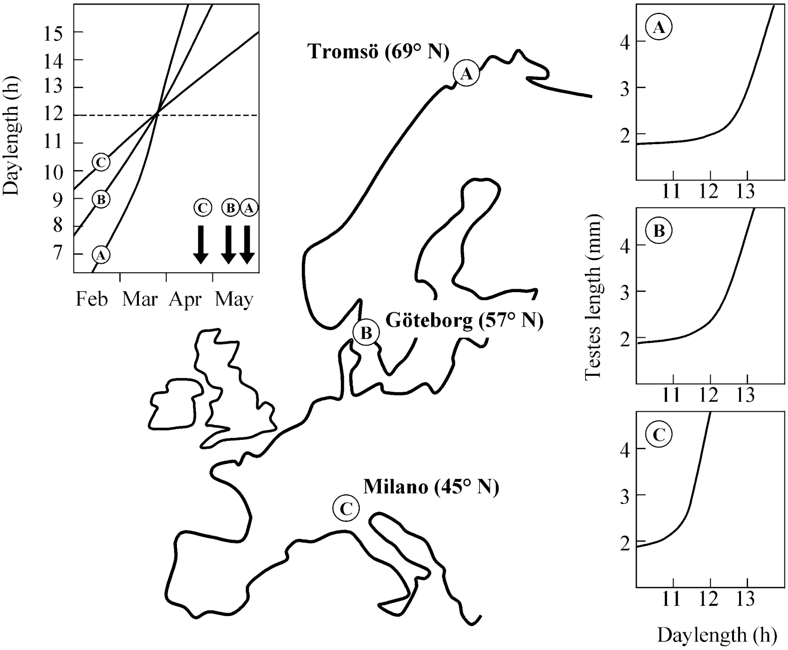

Figure 2 Results from a common garden experiment on male great tits from three different European populations (adapted from Silverin *et al.*, 1993). Birds were collected in winter and transferred to Göteborg (Sweden) where they were kept on short days (8L:16D). All birds were subsequently exposed to an artificial increase in daylength (0.5 h per week) beginning in early January. Diagrams on the right approximate the induced testicular growth in relation to daylength (12 h of light corresponds to week 8 of the experiment). The left diagram shows the changes in daylength the birds would have normally experienced on their respective breeding grounds. The bold arrows show the mean egg-laying dates for each population.

controlled by differences in the responsiveness to photoperiodic stimulation (Lambrechts *et al.*, 1996, 1997). Corresponding results have been obtained on a smaller geographical scale for two adjacent blue tit populations on Corsica (Blondel *et al.*, 1999; Lambrechts *et al.*, 1999). In general, birds which rely on a single, rigid response mechanism for timing reproduction may be unable to immediately track changes in the seasonal availability of food.

Besides phenological changes, range shifts are the most probable and best documented response of birds to global climate change (Walther *et al.*, 2002). Climatic amelioration during the last decades has resulted in a northward expansion of breeding ranges (Burton, 1995; Thomas and Lennon, 1999; Brommer, 2004). At the same time, the wintering areas of some migratory species have shifted northwards (reviewed by Burton, 1995; Berthold, 1998; Fiedler, 2003; Valiela and Bower, 2003). Range shifts are caused by changes in the geographical distribution of suitable climatic conditions and concomitant shifts in resource availability (Root, 1988a,b, 1993). Species follow the environmental conditions they are adapted to and evade areas, which are no longer optimal. Latitudinal range shifts involve changes in photoperiodic conditions. Poleward shifts increase the amplitude of seasonal daylength changes. Birds are bound to respond to these changes.

Most species breeding at mid to high latitude have higher photoperiodic response thresholds than more southerly distributed species, causing a later onset of gonadal recrudescence with increasing latitude. For instance, in European great tits (Figure 2) and various North American *Zonotrichia* species and sub-species the level of sensitivity towards long days is negatively correlated with the species' distributional range, being lowest in the species with the most northerly distribution (Miller, 1960; Lofts and Murton, 1968; Silverin *et al.*, 1993). If global temperature suddenly rises, and if the optimal time for breeding advances, adaptation of the timing of breeding will be most severely constrained in northern temperate species with relatively high photoperiodic response thresholds. On the other hand, if birds of southern origin (e.g., tropical birds) with relatively low thresholds extend their ranges to the north, they will become exposed to steeper vernal increases in daylength, which could result in unseasonably early gonadal development and egg laying. Moreover, longer days encountered at higher latitude in summer could lead to an unseasonably early onset of gonadal regression and photorefractoriness, which would be maladaptive under conditions favouring an extended reproductive period and multiple broods. However, if novel photoperiodic condition bring forth changes in annual rhythmicity that are adaptive under altered climatic conditions, adaptation to environmental change may be facilitated, or even reinforced. The existence of highly adjustable photoperiodic responses that adapt birds to a wide range of different environments is implied by the successful introduction of some European bird species to New Zealand (Cockrem, 1995).

III. RESPONSES TO TEMPORAL AND SPATIAL VARIATION IN PHOTOPERIODIC CONDITIONS

A. Photoperiodic Response of Migrants to Changes in Hatching Date

Spring temperatures in northern temperate regions have considerably increased over the last century (Sparks and Menzel, 2002). In response, numerous bird species are laying their eggs earlier in the year (e.g., Crick and Sparks, 1999; reviewed by Coppack and Both, 2002 and Walther *et al.*, 2002). Earlier egg laying leads inevitably to earlier hatching, since the time for an incubated egg to develop is relatively fixed (but see Cresswell and McCleary, 2003). Unlike birds hatched in midsummer, birds hatching earlier in the year are exposed to short and increasing daylengths during their first days of life and experience the summer solstice at an older age. How do these altered photoperiodic conditions affect the timing of juvenile moult and autumn migration?

The response of the age at onset of autumn migratory activity to differences in hatching date, i.e., photoperiodic conditions, can be described as a reaction norm (Pulido, 2000; Pulido *et al.*, 2001a). Within the range of hatching dates currently found in southern German blackcaps (*Sylvia atricapilla*), the population reaction norm is close to linear (Figure 3). The later a bird hatches, the younger it is when it completes juvenile moult and initiates autumn migratory activity. Acceleration of juvenile development with later hatching is caused by short (or decreasing) daylengths ("calendar effect", Berthold, 1996). Birds hatched earlier in the season experience long daylengths for a longer period, and this causes autumn migration to commence at an older age. However, differences in hatching date are only partially compensated: for every 2 days a blackcap hatches earlier, it is about 1 day older when it initiates migration (Pulido, 2000).

When blackcaps from the southern German breeding population were kept under artificial daylengths simulating 6 weeks earlier hatching, moult ended and migration was initiated at an older age than under natural photoperiodic conditions (Figure 3; Coppack *et al.*, 2001). However, this response was not strong enough to compensate for the simulated advancement of hatching date. The results from this experiment suggest that earlier hatching will inevitably lead to earlier autumn migration. An earlier onset of migration with earlier breeding is likely to be maladaptive in a persistently warming environment (but see Jenni and Kéry, 2003 for the potential advantage of earlier migration in trans-Saharan migrants). Global warming is expected to reduce the probability of cold spells in autumn. Under these conditions, migrants could afford to stay longer on the

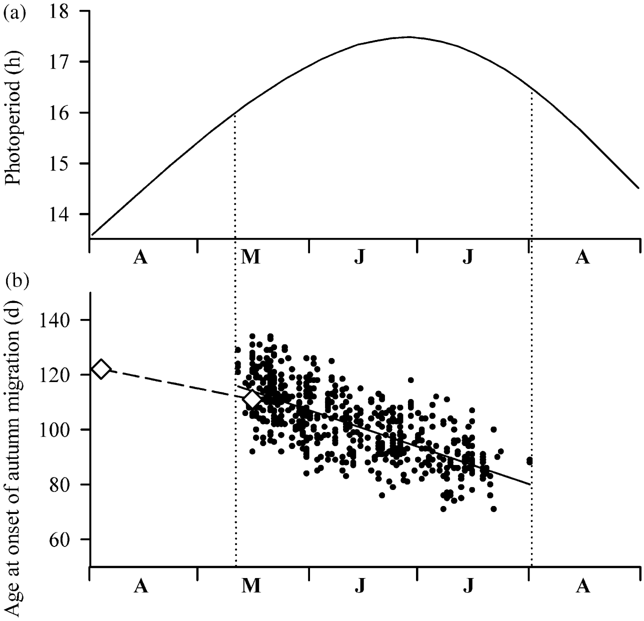

Figure 3 Relationship between hatching date and age at onset of autumn migratory activity as measured under laboratory conditions in southern German blackcaps (*S. atricapilla*) reared in 1988–1997 under natural photoperiodic conditions (top diagram: daylength conditions at 47°50′N latitude). The linear regression (*solid line*) gives the mean population reaction norm (adapted from Pulido, 2000). *Vertical dotted lines* indicate the range of hatching dates under study. The *open symbols* represent the mean onset of autumn migratory activity as measured under simulated early and natural hatching dates in a split brood-experiment (see text and Coppack *et al.*, 2001 for details). The connecting *dashed line* gives the reaction norm outside the current range of hatching dates.

breeding grounds. Later departure in autumn would then allow first-year birds to explore and become familiar with future breeding sites, and to take full advantage of specific food resources used for premigratory fattening—provided food is still available and interspecific competition does not increase. Because photoperiodic responses to conditions outside the current range of hatching dates do not lead to a delayed migration date, extant reaction norms could reduce the fitness benefits of earlier breeding and, as a consequence, slow down life-cycle adaptation to global warming.

In addition, a close correlation between moult and migration (Pulido and Coppack, 2004) might set limits to the independent evolution of breeding and migration phenology. Assuming that current climatic changes favour earlier

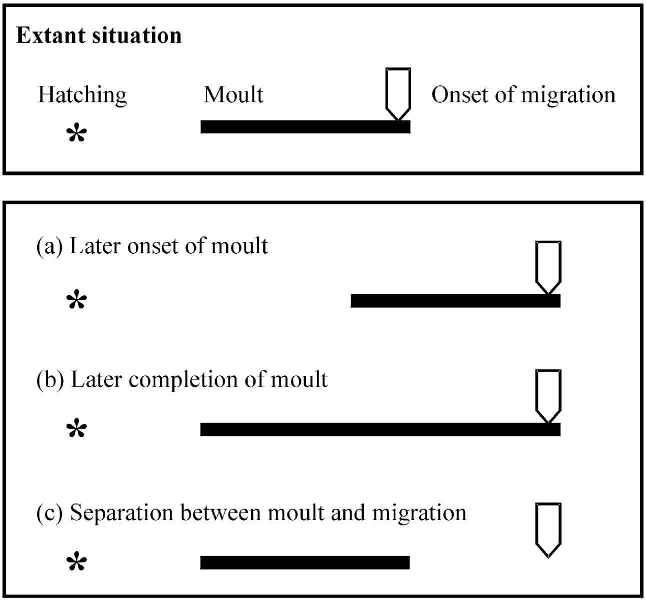

Figure 4 Schematic representation of three possible mechanisms leading to an extension of the time interval between hatching and the onset of autumn migration in juvenile songbirds. They may achieve delayed migration by either (a) postponing the onset of moult, by (b) delaying the completion of moult, causing a prolongation of moult duration, or by (c) increasing the temporal separation of moult and migration. In the presence of high genetic correlation between moult–migration overlap and the onset of migration, as found in the blackcap (Pulido and Coppack, 2004), evolution of delayed onset of migration by mechanisms (b) and (c) may be constrained. If moult and migration are independent processes—or in case of sufficient genetic variation in the phase relationship between moult and migration—a delayed onset of migration could be accomplished by mechanism (c).

breeding and later autumn migration, there are three possible ways birds could change the timing of juvenile moult and the onset of migration relative to hatching date (Figure 4). The first would be to lengthen the interval between hatching and moult. The second potential mechanism would be to increase the duration of moult. Finally, the interval between hatching and onset of migration could be prolonged by extending the time interval between the termination of moult and the onset of migration. Results from a first study investigating the potential for adaptive changes in the timing of moult and migration suggest that in the blackcap, adaptation of the annual cycle may be constrained by unfavourable genetic correlations between the termination of moult and the onset of migration (Pulido and Coppack, 2004). Evolutionary changes in the termination of moult may not lead to adaptive changes in the onset of migration because, as a correlated selection response, the overlap between moult and migration will also be affected. The strong response to artificial selection for older age at onset of migration found in south German blackcaps (Pulido *et al.*, 2001b) was probably achieved by a delayed onset of moult (Figure 4, mechanism a). Significant heritabilities of the age at onset of juvenile moult in the blackcap and other species (Helm and Gwinner, 1999, 2001; Widmer, 1999) suggest that evolutionary change by this mechanism is possible.

The study on the relationship between hatching date and timing of migration in the blackcap illustrates the major problems we face when investigating the evolvability of reaction norms: what are the mechanisms underlying reaction norms? What is the prime target of selection? What determines phenotypic and genetic variability of reaction norms? Generally, we expect evolutionary change in reaction norms to be slow, as empirical and theoretical studies have found that reaction norms have low heritabilities and respond weakly to natural selection (cf. Pigliucci, 2001). However, despite these findings indicating low evolvability, small-scale differentiation in phenotypic plasticity has been found for a number of traits and in different organisms, including birds. In central European garden warblers, for instance, altitudinal variation in the timing of autumn migration is attributable to genetic differences in photoperiodic responsiveness. Population reaction norms appear to be adaptive, reflecting differences in the reliability of daylength as a predictive cue for seasonal changes in food availability in different habitats. Similarly, European blackbirds (*Turdus merula*) from an urban and an adjacent forest population clearly differed in the response of moult onset and duration to variation in hatching date in a common environment, suggesting genetic differences in reaction norms between populations (Partecke, 2002). Variation in the timing and duration of juvenile moult in response to the photoperiod has also been found among sub-species of the stonechat (*Saxicola torquata*) (Helm and Gwinner, 1999, 2001).

If climatic changes persist we expect evolutionary changes in reaction norms, because environmental cues used for synchronising the timing of breeding with maximal food availability may become unreliable (Visser *et al.*, 1998; Both and Visser, 2001; Sanz *et al.*, 2003). However, despite accumulating evidence that photoperiodic responses may differ between adjacent bird populations (Section II), we currently do not know to what extent adaptive changes in reaction norms will keep track with rapid environmental changes. A first quantitative genetic analysis of phenotypic plasticity in the timing of autumn migration in response to hatching date in the blackcap suggests that even though additive genetic variance is present for this trait (Pulido *et al.*, 2001a; Pulido and Berthold, 2003), selection responses may be too weak to allow rapid changes of the population mean.

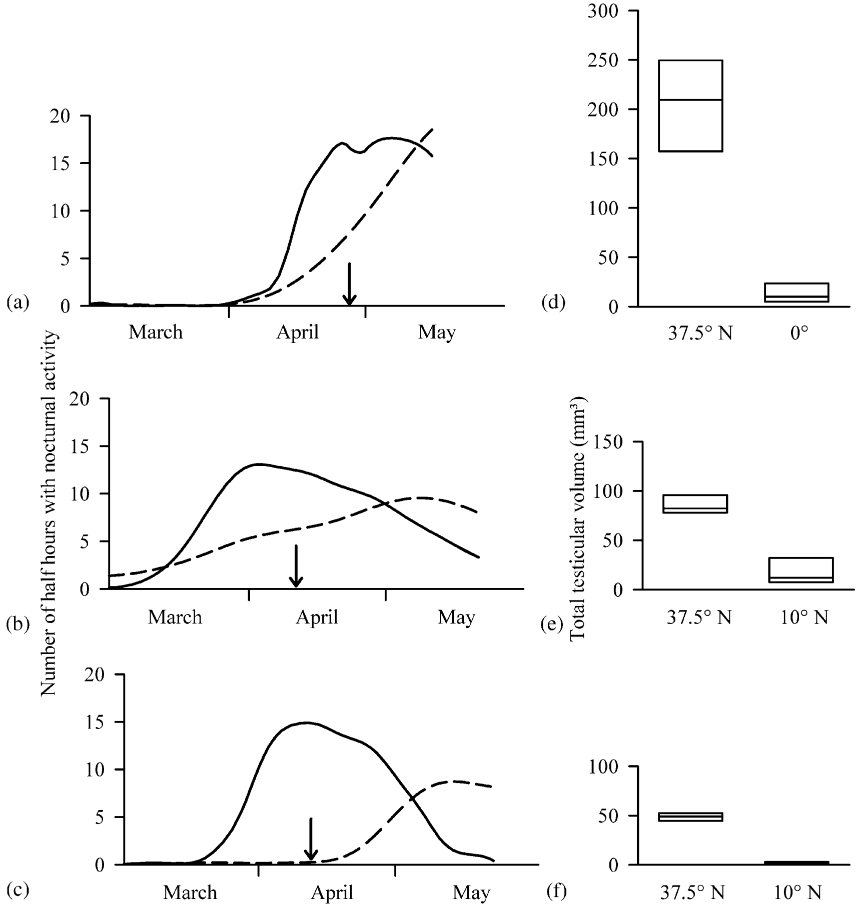

Figure 5 Spring migratory activity and testes volumes measured under laboratory conditions in yearling male garden warblers (a, d), common redstarts (b, e), and pied flycatchers (c, f). 14 garden warblers, 15 common redstarts, and 15 pied flycatchers from south Germany were hand-raised and kept for one year in captivity. At 40 days of age, birds were separated into two groups (treatment and control) in which each family was represented with at least one nest mate. Until the beginning of autumn migration in mid-August, birds of both groups were held under the photoperiodic conditions of their natal area. The treatment group was subsequently exposed to daylengths mimicking migration to and wintering in southern Europe at 37.5°N latitude. The control group was exposed to photoperiodic conditions approximating those experienced in their respective winter ranges in Africa, i.e., at the Equator (garden warbler) and at 10°N (common redstart; pied flycatcher). Light intensity was kept constant at 400 lx during the day, and at 0.01 lx at night. Solid lines in a–c give the conditional mean of nocturnal migratory activity of birds kept on the 37.5°N simulation, dashed lines represent the mean of control birds on African photoperiods. Lines in a–c are locally weighted within optimal bandwidths using the

B. Photoperiodic Response of Migrants to Novel Wintering Ranges

Ever since Rowan's (1925) fundamental discovery that long days in winter induce a change in physiological state (which in turn induces migration to the breeding grounds), researchers have asked whether migratory species have adapted their photoperiodic response mechanism to the diverse photoperiodic conditions experienced during equatorial and trans-equatorial migration (e.g., Hamner and Stocking, 1970; Gwinner, 1987, 1989). In fact, there are only a few experimental studies approaching this question, and even less is known about responses to photoperiodic conditions outside extant breeding and wintering ranges. This information, however, is decisive for predicting whether adaptive changes in migratory behaviour in response to an advancement of spring on the breeding grounds are possible (Coppack and Both, 2002).

If Palaearctic long-distance migrants were able to winter in Mediterranean regions instead of central or southern Africa, their migration routes would be considerably shorter which would allow them to arrive earlier on the breeding grounds and to breed earlier. In fact, the number of Palaearctic-African migrants observed in Mediterranean regions in winter has increased over the last few decades (Berthold, 2001). However, at higher latitudes, Palaearctic-African migrants encounter photoperiodic conditions that are markedly different from those experienced on their traditional African wintering grounds: daylengths decrease more rapidly in autumn, become considerably shorter in winter, and increase at a higher rate in spring (Figure 1). These conditions could potentially impede adaptive changes of the annual cycle. On the other hand, exposure to relatively short days during winter could terminate photorefractoriness at an earlier stage, which in turn would lead to more pronounced responses to the vernal increase in daylength and an advancement of springtime activities. This response to the novel photoperiodic environment would be advantageous under conditions favouring earlier spring arrival and breeding.

The photoperiodic effects of northern wintering has been recently tested in three species of Palaearctic-African passerine migrants—the garden warbler, the common redstart (*Phoenicurus phoenicurus*), and the pied flycatcher (*Ficedula hypoleuca*) (Coppack *et al.*, 2003). Male birds were exposed to photoperiodic conditions simulating wintering north of the Sahara desert at 37.5°N latitude. The three species of migrants responded to the experimental change in wintering area by initiating spring migratory activity earlier and by advancing testicular growth (Figure 5). The northern photoperiodic regime elicited the strongest

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generalised-cross-validation method. Nocturnal (migratory) activity is given in number of half hours with activity. Arrows indicate the dates at which testes volumes were measured non-invasively in birds of both groups. Total testicular volumes are given as Box-plots in d–f (adapted from Coppack *et al.*, 2003).

advancement of spring migratory activity in the pied flycatcher. In all three species, testicular volumes in April—i.e., the time when these species usually arrive on the breeding grounds—were significantly larger in individuals exposed to Mediterranean photoperiods than in nest mates kept under African light-dark cycles. Again, the effect was strongest in the pied flycatcher (Coppack *et al.*, 2003).

These findings are in general agreement with results obtained in a Nearctic trans-equatorial migrant, the bobolink (*Dolichonyx oryzivorus*) (Engels, 1959, 1961). This species breeds in North America and normally stays from November through March in South America, south of the Equator. Male bobolinks kept in an outdoor aviary at 36°N latitude developed beak pigmentation (indicative of gonadal recrudescence) approximately in phase with all-year-round resident species (Engels, 1961). In earlier experiments on bobolinks, Engels (1959) had found that the rate of response to long photoperiods depended inversely on the length of the photoperiod to which males had been exposed previously during the post-nuptial photorefractory phase. Engels (1961) was to conclude that the bobolink could establish a wintering population north of the Equator without readjustment of its photoperiodic control system. However, the precise physiological mechanism underlying this flexible response to daylength remains unknown.

An advancement of life-cycle events with shorter migration distance is in accord with the expected selection response to earlier spring conditions. We therefore expect photoperiodic responses along the latitudinal gradient to reinforce selection for shorter migration distance if temperatures on the breeding grounds continue to rise. Although it is possible that the strength of the photoperiodic response to northern latitudes is maladaptive under the prevailing climatic conditions—as individuals wintering further north may arrive too early on the breeding grounds—we believe that long-distance migrants will gain high fitness benefits from wintering further north and advancing springtime activities under warmer climatic conditions. Similar conclusions have been drawn from blackcaps that have established a new wintering area in the British Isles (Terrill and Berthold, 1990). Over the last decades, an increasing number of blackcaps breeding in continental Europe is overwintering in Britain and Ireland (Langslow, 2002). Birds that winter in Britain rather than in southern Europe are exposed to photoperiodic conditions that promote an earlier termination of photorefractoriness and cause an accelerated onset of vernal physiological condition (Terrill and Berthold, 1990). This response to the novel photoperiodic environment in combination with higher winter survival of blackcaps feeding at bird tables may have facilitated rapid evolution of a novel migration strategy (Terrill and Berthold, 1990; Berthold *et al.*, 1992).

An additional point must be made about the possibility that global warming may cause Palaearctic-African migrants to make even longer journeys than today. At the same time as breeding grounds expand to the north (Thomas and Lennon, 1999), suitable wintering habitats may shift further south due to increasing aridity in the Sahel zone (e.g., Ottosson *et al.*, 2002). Birds may follow suitable breeding and wintering conditions, and by doing so, they will encounter longer and longer photoperiods on either side of the Equator. For some species, however, an expansion of the wintering grounds to the south may be impossible, because daylengths experienced close to and south of the Equator may be too long to permit termination of photorefractoriness. In south German pied flycatchers, for instance, normal annual rhythmicity was developed only under daylengths simulating wintering at 10°N latitude; under photoperiodic condition mimicking migration to wintering areas at 0° and 20°S latitude, prenuptial moult was disrupted, spring migratory activity did not reach full expression, and the gonads remained regressed (Gwinner, 1989). In such a case, a southward expansion or shift of the wintering ranges may only be possible if the photoperiodic response can be adapted to the new conditions. Other species in which photorefractoriness can be broken under conditions exceeding equatorial daylength (approx. 12.8 h), as in the garden warbler (Gwinner, 1987; Gwinner *et al.*, 1988), may succeed in extending their wintering ranges to the south.

C. Tropical Birds and Their Potential for Poleward Range Extension

For non-migratory tropical birds, a sudden shift in global climate patterns may represent a potential threat. Many tropical species living in seemingly constant environments breed seasonally and may even respond to the slight annual changes in daylength experienced close to the Equator (Hau *et al.*, 1998). How will tropical birds respond to the high-amplitude changes in daylength that are found outside current breeding ranges? Are tropical species limited in their potential for range shifts and expansions?

In African stonechats (*S. t. axillaris*), complete cycles of moult and gonadal growth can be elicited by sinusoidal photoperiodic changes (Gwinner and Scheuerlein, 1999). Equatorial stonechats behave essentially like temperate-zone stonechats (*S. t. rubecula*) when held on daylengths simulating conditions at 47.5°N latitude. Thus, the crude response to sinusoidal changes in daylength appears to be conserved in the stonechat, independent of the sub-species' origin or present migratory status. Gwinner and Scheuerlein (1999) have suggested that this potential for adaptive photoperiodic response may be a consequence of this tropical population having been founded by individuals from northern populations, or attributed to interbreeding with northern migrants from the same species. These hypotheses imply that highly adjustable photoperiodic systems can only evolve at higher latitudes and that extant tropical populations may possess photoperiodic adaptability only if they are genetically related to these populations. If this is true, many tropical bird species may be unable to alter their current distributions by adjusting to novel seasonal environments. A limited capacity for adaptive response to photoperiodic conditions outside the tropics has been experimentally demonstrated in the equatorial Andean sparrow (*Z. capensis*). Unlike its north-temperate relatives (*Z. leucophrys*, *Z. atricapilla*, and *Z. albicollis*), the Andean sparrow has no photoperiodic response mechanism for effectively preventing late summer and autumn breeding under northern seasonal conditions (Miller, 1965).

D. Birds in Urban Habitats and the Effect of Artificial Light

With increasing urbanisation and the introduction of outdoor lighting, light pollution has considerably increased in the last decades (Riegel, 1973; Cinzano *et al.*, 2001). As a result, birds living in or near highly urbanised or industrialised areas are exposed at night to increasing levels of artificial light. Several bird species have been reported to prefer habitats with night-illumination (e.g., Rees, 1982; Gorenzel and Salmon, 1995) and to be attracted, or disoriented, by artificial light sources during migration (e.g., Cochran and Graber, 1958; Drost, 1960; Avise and Crawford, 1981; Martin, 1990; Jones and Francis, 2003). Diurnal birds exposed to artificial light may become more active and extend their feeding periods into the night (e.g., Goertz *et al.*, 1980; Nein, 1989; Frey, 1993). In addition to these immediate effects, an artificial prolongation of daylength can have profound effects on the organisation of avian life cycles (Luniak and Muslow, 1988; Schmidt, 1988; Partecke, 2002). This has been most intensively studied in European blackbirds (*T. merula*). The breeding season in blackbirds living in urban habitats starts earlier and ends later than in blackbirds in rural habitats. Moreover, urban birds moult earlier and more extensively and show a reduced tendency to migrate (Luniak and Muslow, 1988; Luniak *et al.*, 1990; Partecke, 2002). Among-habitat differences in life-history traits may not only be attributed to differences in light regimes but also to differences in temperature, density, or food availability. In a common garden experiment, Partecke (2002) studied the effects of photoperiodic response and genetic differences on breeding, moult, and migration in urban and forest-dwelling blackbirds. His results suggest that among-population differences in the timing of gonadal recrudescence are predominantly an effect of different photoperiodic conditions. Differences in the timing of moult can be attributed to (genetic) differences in the response to the photoperiod. Differentiation in the amount of autumn migratory activity is most likely due to genetic differences. Thus, life-cycle adaptation to urban environments may involve phenotypic plastic responses, genetic changes in plasticity, and genetic responses.

The response of birds living in urban habitats to artificial light may have important consequences for their adaptation to climate change. Light pollution may induce earlier breeding, which may be favourable under improved conditions in spring (see above sections), and thus may facilitate adaptation to climatic amelioration. However, as anthropogenic light regimes are not necessarily related to the availability of food, the timing of breeding may be shifted towards a period in which appropriate food is scarce or missing (see, for instance, Schmidt and Steinbach, 1983; Schmidt and Einloft-Achenbach, 1984). This desynchronisation between the timing of breeding and the availability of food would lead birds into evolutionary traps (cf. Schlaepfer *et al.*, 2002), similar to the expected effect of rapid phenological change on birds living under natural photoperiodic conditions (Stenseth and Mysterud, 2002).

IV. CONCLUSION

Birds, like any other highly mobile organism, may respond to global climatic changes either by evading the altered environment or by adapting to local conditions. We stress that the response to the photoperiodic environment is a crucial factor determining to what extent range shifts and adaptive evolution will be possible. Climate change is currently altering the phenology of many organisms, but at different rates. Poikilothermic organisms may immediately respond to temperature changes. In contrast, homiothermic animals, like birds, that use temperature-independent (i.e., photoperiodic) cues to time their life cycles may get out of phase with the selective environment. In environments that have suddenly changed due to human activity, photoperiodic cues might no longer lead to adaptive responses. However, if photoperiodic conditions outside a species' or population's current range elicit phenotypic changes that are favoured by selection, range shifts and colonisation of new habitats may be facilitated. We conclude that any study on the adaptability of birds to human-caused environmental changes should take into account that adaptive processes may be facilitated or constrained by physiological and behavioural responses to the photoperiodic environment.

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