

Photoperiodic response may facilitate adaptation to climatic change in long-distance migratory birds

Timothy Coppack^{1*}, Francisco Pulido¹,
Michael Czisch², Dorothee P. Auer²
and Peter Berthold¹

¹Max Planck Research Centre for Ornithology, Andechs & Radolfzell, Vogelwarte Radolfzell, 78315 Radolfzell, Germany

²Max Planck Institute of Psychiatry, Nuclear Magnetic Resonance research group, Kraepelinstrasse 2-10, 80804 Munich, Germany

* Author and address for correspondence: Institute for Avian Research, 'Vogelwarte Helgoland', Inselstation, PO Box 1220, 27494 Helgoland, Germany (coppack@vogelwarte-helgoland.de).

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Recent climatic change is causing spring events in northern temperate regions to occur earlier in the year. As a result, migratory birds returning from tropical wintering sites may arrive too late to take full advantage of the food resources on their breeding grounds. Under these conditions, selection will favour earlier spring arrival that could be achieved by overwintering closer to the breeding grounds. However, it is unknown how daylength conditions at higher latitudes will affect the timing of life cycle stages. Here, we show in three species of Palaearctic–African migratory songbirds that a shortening of migration distance induces an advancement of springtime activities. Birds exposed to daylengths simulating migration to and wintering in southern Europe considerably advanced their spring migratory activity and testicular development. This response to the novel photoperiodic environment will enable birds wintering further north to advance spring arrival and to start breeding earlier. Thus, phenotypic flexibility in response to the photoperiod may reinforce selection for shorter migration distance if spring temperatures continue to rise.

Keywords: adaptive evolution; circannual rhythms; *Ficedula hypoleuca*; *Phoenicurus phoenicurus*; reaction norm; *Sylvia borin*

1. INTRODUCTION

Many organisms use daylength as an environmental cue to initiate activities such as flowering, breeding or migration in anticipation of annual seasonal changes (Gwinner 1986). Species that rely on photoperiodic cues are expected to suffer from climate change because extant responses might be maladaptive under novel environmental conditions (Coppack *et al.* 2001; Schlaepfer *et al.* 2002). Birds breeding at mid- to high latitudes may become desynchronized with temperature-dependent peaks in food abundance, which are essential for successfully rearing their young (Visser *et al.* 1998). Long-

distance migrants will be particularly affected by shifts in food availability because they spend only a short period on the breeding grounds and therefore are under strong selection for an optimal timing of seasonal events. Recently, it was shown that in the pied flycatcher (*Ficedula hypoleuca*) egg laying became earlier between 1980 and 2000, but that this advancement was not sufficient to track the earliness of spring, most probably because their arrival dates had not changed (Both & Visser 2001). Despite considerable amounts of additive genetic variation in the timing and distance of migration (Pulido & Berthold 2003) and flexibility in the timing of spring migration towards large-scale climatic fluctuation (Hüppop & Hüppop 2003), it is uncertain whether long-distance migrants will succeed in sufficiently advancing spring arrival if spring temperatures continue to rise (Coppack & Both 2003). Earlier spring arrival could be achieved by wintering closer to the breeding grounds, e.g. in Mediterranean regions instead of central Africa—as has recently been reported for some bird species (Berthold 2001). However, the range of photoperiods under which successive stages of the circannual cycle (i.e. moult, migration, reproductive maturation) can be completed may be limited (Gwinner 1996). In trans-Saharan long-distance migrants, a shortening of migration distance would involve a dramatic change in photoperiodic conditions that could disrupt annual rhythmicity.

Here, we show that Palaearctic long-distance migrants advance breeding if they winter closer to the breeding grounds, as a consequence of the novel photoperiodic environment experienced during the non-breeding season.

2. MATERIAL AND METHODS

We conducted indoor experiments on three Palaearctic songbird species from three different families: the garden warbler (*Sylvia borin*), the common redstart (*Phoenicurus phoenicurus*) and the pied flycatcher. These species breed throughout Europe and migrate across the Sahara desert to central and southern Africa during the non-breeding period (Moreau 1972). We kept hand-raised male birds during their first winter either under daylengths simulating a potential wintering area north of the Sahara or under photoperiods mimicking conditions in their actual wintering site in central Africa. We compared the time course of migratory activity with testes sizes (an indicator of reproductive maturity) at a given time in spring.

(a) *Birds*

We collected 14 male garden warblers from seven nests hatched near Radolfzell (47°44' N, 8°58' E) and Mannheim (49°29' N, 8°29' E) between 27 May and 8 June 1999 (median: 3 June). In the following year, we took 15 male common redstarts from five nests hatched between 14 May and 19 May (median: 17 May) in the surroundings of Stuttgart (48°46' N, 9°11' E), and 15 male pied flycatchers from four nests hatched on 18 May near Erlangen (49°36' N, 11°0' E). Nestlings were sexed by molecular methods (cf. Griffiths *et al.* 1996) and transferred at an age of 5–7 days (garden warbler) or 8–11 days (common redstart; pied flycatcher) to our institute in Radolfzell. They were hand-raised and kept in a climate chamber at 26 ± 1.5 °C. At 30 days of age, birds were moved to individual registration cages (45 cm × 23 cm × 38 cm) where they had food and water *ad libitum*, and were kept at 20 ± 1.5 °C.

(b) *Photoperiodic treatments*

At 40 days of age, birds were separated into two groups (treatment and control group) in which each family was represented with at least one nestling. 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 southern Europe (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 10° N (common redstart; pied flycatcher) and at the Equator (garden warbler) (figure 1a). Both groups were held under these simulated conditions until all individuals had initiated spring migratory activity. We defined the time between the beginning

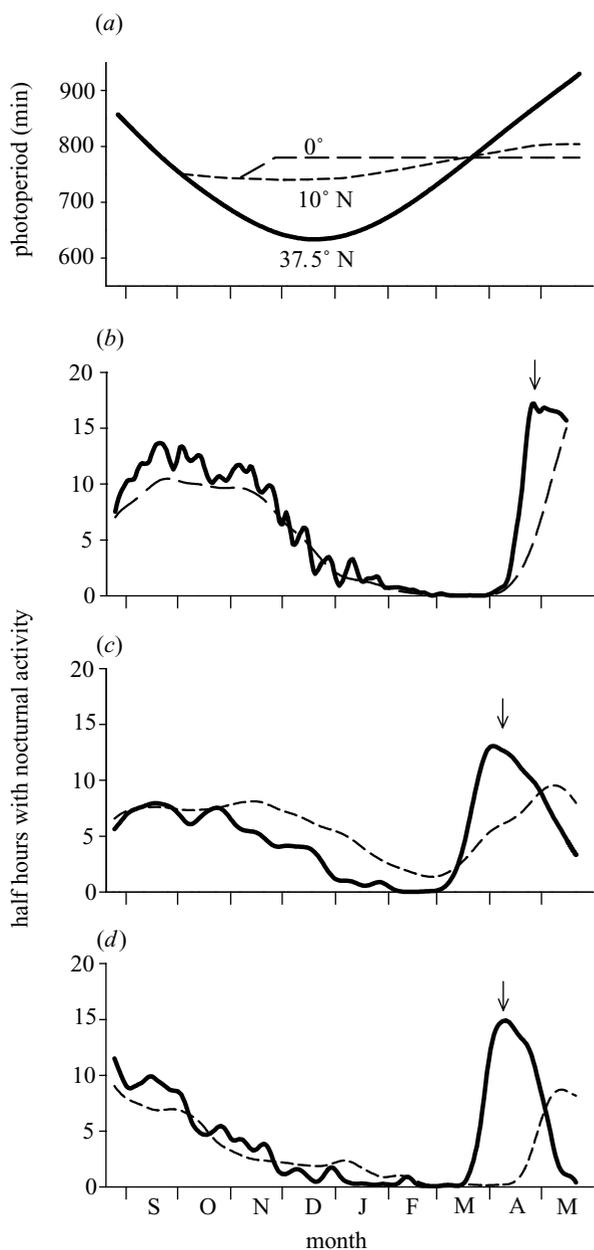


Figure 1. The effect of daylength on the timing of migratory activity in three species of songbirds. (a) Photoperiodic treatments simulating various wintering latitudes. (b–d) Patterns of migratory activity as recorded under laboratory conditions from September to May in (b) garden warbler, (c) common redstart and (d) pied flycatcher. Solid lines show the conditional mean of nocturnal migratory activity of birds kept on a photoperiodic regime simulating wintering at 37.5° N latitude; dashed lines show the mean of control birds on African photoperiods (0°, garden warbler; 10° N, common redstart and pied flycatcher). All lines in (b)–(d) are locally weighted within optimal bandwidths using the generalized-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 in both groups.

and the end of civil twilight as effective daylength. Light intensity was kept constant at 400 lx during the day, and at 0.01 lx at night. The timetables for the beginning and end of civil twilight at different latitudes (1 hour east of Greenwich) were provided by the Astronomical Applications Department of the US Naval Observatory, Washington (cf. <http://aa.usno.navy.mil>).

(c) Measures

From August to May, locomotory activity was continuously recorded in cages equipped with two movable perches connected to microswitches. Electrical impulses were transmitted to an event recorder that registered the number of movements per unit of time. We used the number of half-hour intervals with nocturnal activity as a measure to quantify migratory activity (i.e. migratory restlessness, or Zugunruhe; cf. Berthold 2001). For each bird, the onset of spring migratory activity was defined as the first night on which it was active during at least five half-hour intervals. We measured total testicular volumes once in garden warblers on 28–29 April, and once in pied flycatchers and common redstarts on 9–10 April. Testicular volumes were determined non-invasively using magnetic resonance imaging. Scans were performed on a Bruker Biospec 70/30 imaging system operating at 7 T (for details, see Czisch *et al.* (2001)).

(d) Statistical analyses

Both variables, i.e. testicular volume and onset of migratory activity, did not significantly deviate from normality. We therefore tested the effects of the photoperiodic treatment on these variables using parametric methods. In the analyses of variance, species and photoperiodic treatment were entered as fixed effects. Error probabilities in ANOVAs were based on type III sums of squares throughout.

3. RESULTS

The three species of Palaearctic migrants significantly responded to the simulated changes in wintering area by initiating spring migratory activity earlier (ANOVA: $F_{1,35} = 55.48$, $p < 0.001$) and by advancing testicular growth, as indicated by significantly larger testes in spring (ANOVA: $F_{1,38} = 104.73$, $p < 0.001$). The responses to the Mediterranean photoperiod, however, differed among species both in the onset of migratory activity (figure 1; species-by-treatment effect, $F_{2,35} = 15.15$, $p < 0.001$) and in spring testicular volume (table 1; species-by-treatment effect, $F_{2,38} = 19.74$, $p < 0.001$). The northern photoperiodic regime elicited a strong advancement of the onset of spring migratory activity in garden warblers ($\Delta_t = 13.7$ days, $t_{12} = 3.08$, $p = 0.01$) and pied flycatchers ($\Delta_t = 33.1$ days, $t_{13} = 13.17$, $p < 0.001$). The response of the common redstart to the altered photoperiod was considerably smaller, but in the same direction ($\Delta_t = 2.9$ days, $t_{10} = 0.63$, $p = 0.54$). In all three species, testicular volumes in April—i.e. the time at which 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 (table 1; figure 2). Again, the effect was strongest in the pied flycatcher (a 19-fold increase in size) and smallest in the common redstart (a fourfold increase).

4. DISCUSSION

Our results show that the relatively short daylengths experienced during northern wintering may cause an advancement of spring migratory activity and testicular growth, even in long-distance migrants, i.e. birds that were previously considered to be mainly stimulated by long days (e.g. Gwinner *et al.* 1988). The consistency of our findings in three species of Palaearctic–African migrants from different families (Sylviidae, Turdidae, Muscicapidae) suggests that the response to short daylengths—known to promote the termination of photorefractoriness in temperate-zone species (Nicholls *et al.* 1988)—is common in songbirds and has an adaptive function. As range shifts have occurred

Table 1. Spring testicular volumes in three species of long-distance migratory songbirds exposed to daylengths simulating wintering in southern Spain or central Africa.

(Testicular volumes (arithmetic means \pm s.d. given in mm^3) were measured once on 28–29 April (garden warbler) and 9–10 April (common redstart; pied flycatcher). Sample sizes are given in parentheses; the equality of means was tested using *t*-tests.)

species	total testicular volume (mm^3)			<i>p</i>
	Spain	Africa	difference	
garden warbler	195.8 \pm 69.9 (8)	12.8 \pm 9.8 (6)	183.0	< 0.001
common redstart	83.6 \pm 7.5 (8)	18.8 \pm 15.1 (7)	64.8	< 0.001
pied flycatcher	47.8 \pm 7.9 (8)	2.5 \pm 1.1 (7)	45.3	< 0.001

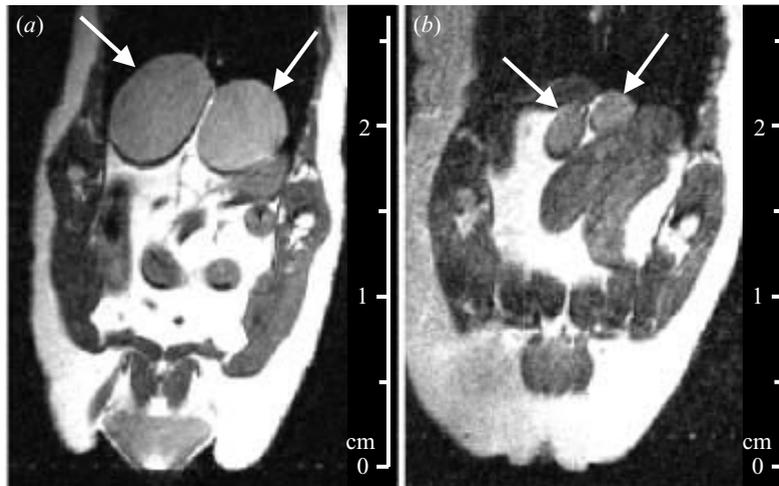


Figure 2. Cross-sectional magnetic resonance images (taken on 28 April) showing the testes (arrows) of two representative garden warblers (nest-mates) after exposure to (a) Mediterranean or (b) African photoperiods during winter.

frequently throughout the evolutionary history of birds, most taxa may have developed or retained photoperiodic responses that enable them to winter at different latitudes. We hypothesize that, as far as the photoperiodic control mechanism is concerned, long-distance migrants could establish wintering populations further north, without readjustment of this mechanism. This conclusion is in accordance with the finding of Engels (1961) in a trans-equatorial migrant, the bobolink (*Dolichonyx oryzivorus*). Bobolinks held throughout the winter and spring in an outdoor aviary at 36° N latitude developed beak pigmentation (indicative of gonadal recrudescence) approximately in phase with locally wintering songbird species. Further support comes from an experimental study on migratory blackcaps, *Sylvia atricapilla*, which advanced gonadal growth and the onset of spring migration under photoperiodic conditions simulating wintering in the UK instead of southern Europe (Terrill & Berthold 1990).

Decreasing migration distances, earlier spring arrival and later departure in autumn are the expected and observed changes in migratory behaviour in response to recent climatic change (Berthold 2001; Walther *et al.* 2002; Fiedler 2003; Hüppop & Hüppop 2003). Our results indicate that a shortening of migration distance will result in earlier northward migration and earlier breeding. In Palaearctic long-distance migrants, an establishment of overwintering areas north of the Sahara will lead to considerably earlier spring arrival, as a result of the shorter migration distance and the advancement of spring

migratory activity induced by the novel photoperiodic environment. Although this correlated response to wintering latitude could be maladaptive under the prevailing climatic conditions—as these birds could arrive on the breeding grounds too early—we expect long-distance migrants to gain high fitness benefits from wintering further north and advancing springtime activities if spring temperatures on the breeding grounds continue to increase. Earlier breeding in response to global warming is currently observed in several nearctic and Palaearctic breeding birds (reviewed by Walther *et al.* (2002)), and selection for earlier breeding has increased over the last few decades (Visser *et al.* 1998; Both & Visser 2001). Thus, in view of recent climatic trends, we expect extant photoperiodic responses to reinforce selection for shorter migration distance.

For migratory species that have not yet established wintering populations north of the Sahara, adaptation to an altered phenology on the breeding grounds will be difficult, if not impossible, and will take much longer. Selection for earlier breeding will necessitate evolutionary changes in the timing of spring migration, i.e. earlier departure from the wintering grounds, or faster migration (Coppack & Both 2003), and changes in the timing of gonadal growth. A gradual decrease in migration distance will not be possible because suitable habitats for wintering within and close to the Sahara are extremely scarce. The evolution of populations with shorter migration distances will be possible only through an ‘evolutionary jump’ over

the Sahara (cf. Pulido *et al.* 1996) and may be achieved in only large populations with sufficient genetic variation in migration distance (Pulido & Berthold 2003).

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