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Can long-distance migratory birds adjust to the advancement of spring by shortening migration distance? The response of the pied flycatcher to latitudinal photoperiodic variation

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Abstract

Many organisms use day length as a cue for synchronizing their life cycles with seasonal changes in environmental productivity. Under rapid climate change, however, responses to day length may become maladaptive, and photo-responsive organisms may only be able to evade increasingly unsuitable habitats if they can accommodate to a wide range of photoperiodic conditions. A previous experiment showed that the pied flycatcher, *Ficedula hypoleuca*, a Palaearctic-Afrotropical migratory bird, would strongly advance the timing of spring migration and reproductive maturation if it shifted its wintering area from sub-Saharan Africa to the Mediterranean region. However, it is unknown whether this marked response to latitudinal variation in photoperiodic conditions is continuous over the entire range of potential wintering areas, and if a shortening of migration distance would be an effective mechanism to adjust the timing of migration to rapidly changing climatic conditions. Here, we experimentally show that a moderate northward displacement of the pied flycatcher's current wintering grounds by 10° would result in a clear advancement of the termination of prenuptial moult and the initiation of spring migratory activity and gonadal growth. However, we found no further advancement under conditions simulating higher wintering latitudes, suggesting the existence of a critical photoperiodic threshold or a steep gradual response within a narrow geographical range between 10° and 20° northern latitude. Because habitat conditions in this area are deteriorating rapidly, the potential for pied flycatchers to adjust their life cycle to changing climatic conditions by shortening the migration distance may be limited in the future.

Keywords: adaptation, circannual rhythm, *Ficedula hypoleuca*, migration, moult, phenotypic plasticity, photoperiodism, reaction norm

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Introduction

Organisms living in seasonal habitats often rely on indirect environmental cues to match life history or behavioural decisions with favourable ecological conditions. At mid- to high-latitude, the annual change in day length (photoperiod) provides the most predictive source of spatio-temporal information about the envir-

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onment and is used by most organisms as an initial predictive cue for synchronizing life-cycle events with seasonal changes in resource availability (Wingfield & Kenagy, 1991; Dawson *et al*., 2001; Bradshaw & Holzapfel, 2007).

The major effect of recent climatic change on biotic systems is the modification of the timing and length of the growing season (Bradshaw & Holzapfel, 2008), which sets the time window for successful reproduction (Visser *et al*., 2004). Unlike temperature, the seasonal change in day length is not affected by climate change. Consequently, organisms that rely on photoperiodic cues to time their life cycles, like the majority of seasonally breeding and migrating birds (Dawson *et al*., 2001), may experience reduced fitness when their phenology no longer tracks the changing environment (Coppack & Pulido, 2004; Visser *et al*., 2004; Dawson, 2008; Visser, 2008). Such dissociation between the response to predictive cues and selective environment can lead to population declines and extinctions, irrespective of the availability of suitable habitats (i.e. evolutionary traps; Schlaepfer *et al*., 2002).

Long-distance migratory songbirds, such as the pied flycatcher, *Ficedula hypoleuca*, have been shown to be affected by multiple factors associated with climate change, especially changes in the seasonal availability of invertebrate food relative to the timing of arrival at the breeding grounds (Coppack & Both, 2002; Both *et al*., 2006; Pulido, 2007). There are indications that in some regions, populations of pied flycatchers are suffering from the rapid advancement of spring. In a Dutch pied flycatcher population, selection for earlier egg-laying dates increased over a 20-year period of climatic warming (Both & Visser, 2001). Yet, although egg-laying advanced on an average, pied flycatchers did not arrive earlier and, therefore, did not reproduce early enough to take full advantage of the peak in caterpillar abundance used for chick rearing (Both & Visser, 2001; Both *et al*., 2006).

It has been suggested that insectivorous long-distance migrants such as the pied flycatcher could adjust to altered phenological conditions on the breeding ground by an adaptive shortening of migration distance (Coppack & Both, 2002; Coppack *et al*., 2003; Pulido, 2007). This would require a fine-tuned response of the annual life cycle to latitudinal changes in photoperiodic conditions. We have previously shown in three trans-Saharan migratory songbird species that photoperiodic conditions north of the Sahara Desert elicit a pronounced advancement of spring migratory disposition and testicular maturation (Coppack *et al*., 2003). The pied flycatcher, the species with the strongest response, would in effect initiate spring migration and reproductive maturation approximately 1 month earlier after wintering in the Mediterranean region, solely as a response to the altered photoperiodic environment (Coppack *et al*., 2003). However, such a shift in wintering area would only be possible by a large 'evolutionary jump' across an extensive ecological barrier, the Sahara Desert, which, if possible at all, would require many generations of selection (Pulido *et al*., 1996; Pulido, 2007). Moreover, an advancement of migration and reproduction by 1 month, in conjunction with the abbreviated migration, may be a change too large to be adaptive, even under the current rates of temperature increase in the breeding areas in spring (Coppack *et al*., 2003; Coppack & Pulido, 2004). We therefore need to know the shape of the norm of reaction over a wide range of wintering areas to be able to assess the potential and limitations for the advancement of spring arrival and reproduction through a gradual reduction of migration distance from present-day African wintering grounds.

In the present study, we experimentally analysed the pied flycatcher's phenotypic response across a latitudinal photoperiodic cline with the aim of assessing the shape and breadth of the mean populational reaction norm.

Methods

Birds

The pied flycatcher is a small insectivorous songbird that breeds throughout Europe and migrates to tropical Africa in winter. Compared with the species' vast breeding distribution, its wintering area is restricted to a narrow band along the West African coast from the equator to approximately 15°N (Lundberg & Alatalo, 1992; Veen *et al*., 2007). In 2000, we collected 15 male pied flycatchers from four broods hatched near Erlangen, Germany (49°36′N, 11°01′E) on 18 May (see Coppack *et al*., 2003). In 2002, we collected an additional 21 male birds from seven broods of the same population hatched on 26–30 May (median 26 May). Nestlings were sexed by molecular methods (cf. Griffiths *et al*., 1998) and transferred at an age of 8–11 days to the laboratory in Radolfzell (47°44′N, 8°58′E). Birds 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 *ad libitum* food and water and were kept at 20 ± 1.5 °C for 1 year (for details on feeding and maintenance conditions, see Pulido & Coppack, 2004).

Photoperiodic simulations

Until the start of autumn migration in mid-August, all birds were held under the photoperiodic conditions of their natal area. Following the identical protocol of our previous experiment (Coppack *et al*., 2003), birds were assigned to treatment groups, in which each family was represented by at least one nestling and exposed to day length conditions simulating migration to different wintering latitudes. Birds of the present study were allocated to three photoperiodic treatments simulating wintering latitudes at 20°N, 30°N and 50°N, respectively (Fig. 1).

As in previous studies, effective day length was defined as the time between the beginning and the end of civil twilight (defined as the time when the centre of the sun is 6° below the horizon). Light intensity was kept constant at 400 lx during daytime and at 0.01 lx at night, with no simulation of dusk or dawn periods. The timetables for the beginning and the end of civil twilight at different latitudes (1 h east of Greenwich) were provided by the Astronomical Applications Department of the US Naval Observatory, Washington (cf. http://aa.usno.navy.mil). Light periods were changed in 5-min steps using automatic time switches.

Measurement of migratory activity, moult and gonadal development

From August to May, locomotory activity was continuously recorded in cages equipped with two movable perches connected to micro-switches. Electric 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 (Coppack *et al*., 2003).

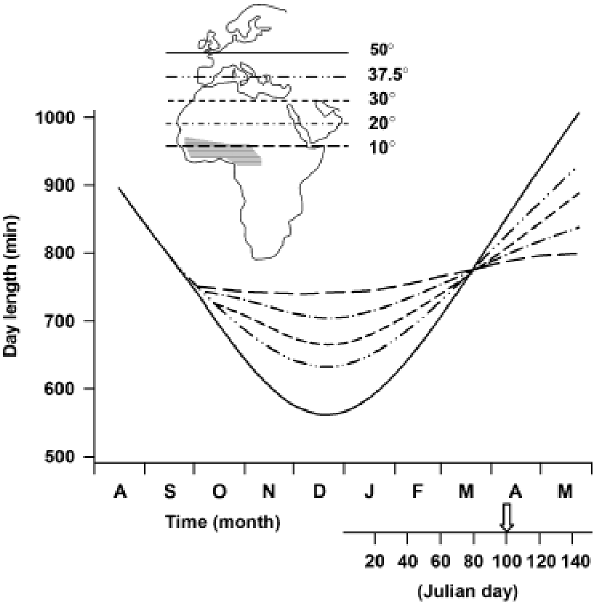

Fig. 1 Experimental photoperiodic conditions simulating migration to different wintering latitudes ranging from 10°N (i.e. the current wintering range of the pied flycatcher in Africa indicated as grey area) to 40°N, as well as year-round residency at 50°N (i.e. the breeding latitude of the population from which experimental birds were sampled). Day length is defined as the time between the onset of civil twilight in the morning and the end of civil twilight in the evening. The arrow on the time axis indicates the date of measurement of testis size.

The progress of moult was measured by inspecting the birds in weekly intervals. Moult protocols were made separately for body plumage and the 20 primary and 12 secondary flight feathers. We determined the progression of moult by weekly inspecting 21 different body feather tracts in each individual bird as described by Berthold *et al*. (1970).

In spring, we estimated the size of the birds' gonads, which is a good proxy for reproductive readiness in birds (Dawson *et al*., 2001). Testicular size was measured noninvasively using magnetic resonance imaging (details described in Czisch *et al*., 2001) for which birds were temporally moved from their housing in Radolfzell, Germany, to the University of Antwerp, Belgium, on 11/12 April 2003. To render estimates of testis size from our previous study (Coppack *et al*., 2003) comparable, magnetic resonance images from both studies were reanalysed, defining testis size as the largest area of testicular tissue visible in cross-sectional images.

Statistical analyses

For obtaining a complete reaction norm, i.e. testing the response to potential wintering sites from the extant wintering area to the current breeding area at a 10°-scale, data from the current study were pooled with those of the earlier study (Coppack *et al*., 2003), after standardizing the methods of scoring testis size. Most measured variables were normally distributed or deviated only slightly from normality ('onset of migratory activity' and 'termination of moult'). To obtain better properties for statistical testing, we log-transformed 'termination of moult' and made an inverse transformation of the variables 'duration of moult' and 'onset of migratory activity'. The effect of our simulation of different latitudes on the response variables was tested using mixed models (PROC MIXED) in SAS, whereby we controlled for 'hatching date' and 'family' effects.

Results

The exposure of pied flycatchers to a series of simulated photoperiodic conditions to the north of their extant wintering range had clear effects on the timing of moult, migration and gonadal growth (Table 1, Fig. 2). All

Table 1 Results of mixed-model ANOVA

Source of variation	df	SS	F	P
Onset of moult				
Latitude	3	1045	1.30	0.321
Family	9	1875	0.78	0.639
Family × Latitude	11	2951	1.80	0.171
Termination of moult [ln]				
Latitude	3	0.011	8.86	0.003
Family	9	0.049	1.35	0.312
Family × Latitude	11	0.042	2.28	0.094
Duration of moult [inv]				
Latitude	3	1.47×10^{-4}	0.47	0.709
Family	9	1.35×10^{-3}	1.44	0.278
Family × Latitude	11	1.15×10^{-3}	2.55	0.068
Separation between moult and migration				
Latitude	3	524.5	3.76	0.044
Family	9	579.0	1.37	0.306
Family × Latitude	11	515.3	1.77	0.189
Onset of migratory activity [inv]				
Latitude	3	3.09×10^{-5}	60.4	<0.001
Family	9	2.92×10^{-6}	1.9	0.149
Family × Latitude	12	2.04×10^{-6}	0.8	0.660
Testis size				
Latitude	3	569.5	23.19	<0.001
Family	9	168.2	2.37	0.112
Family × Latitude	9	66.1	3.79	0.047

Latitude is treated as a fixed effect and family as random effect.

measured variables, with the exception of the onset and duration of prenuptial moult, were affected by the simulated photoperiods (Table 1). Compared with the control group held at a photoperiodic regime at 10°N, birds ended prenuptial moult significantly earlier (by 18–23 days) and advanced migration onset (by 25–33 days) in all experimental groups (Table 1). However, there were no significant differences in the termination of moult and the onset of migration among birds kept under photoperiodic conditions beyond 10°N latitude, indicating a threshold response to latitudinal photoperiodic variation (Fig. 2).

Significantly larger testes than that in the control group were found only in the two groups kept under the northernmost conditions (37.5°N and 50°N). The differences in testes size between the 20°N and 30°N groups and the 10°N group were not statistically significant (Dunnett's C test: $P = 0.164$ and 0.109, respectively), but testes sizes in these two groups were lower than in the two northern groups (Dunnett's C test: $P < 0.01$, see Fig. 2).

Individuals from different families differed in their response of gonadal development to photoperiodic regimes as indicated by the significant family-by-latitude interaction effect (Table 1). This was particularly apparent in the 20° and 30° groups, where the variance in gonadal size was larger than in the other experimental groups (Leven's test for equality of variances: $P < 0.05$). Under these photoperiodic regimes, individuals from some families had hardly initiated testicular growth, while birds from other families had almost fully grown testes (see Fig. 2d).

Discussion

In view of recent environmental changes favouring earlier spring migration (Coppack & Both, 2002; Fiedler, 2003; Pulido, 2007), our experiments aimed at studying the effects of latitudinal shifts in the wintering area on the timing of life-cycle stages in a long-distance migratory songbird. We had previously demonstrated that a northward shift of the wintering latitude from 10°N to 37.5°N would result in a considerable advancement of the timing of spring migration and gonadal growth (Coppack *et al*., 2003). Here, we show that the response to latitudinal displacement does not affect all life-cycle stages equally. While the termination of prebreeding moult, the onset of migration and the timing of gonadal growth were strongly advanced, there was no response in the onset and duration of prebreeding moult. This suggests that the advancement of life-cycle events may have been caused by day length conditions experienced around the vernal equinox (Fig. 1), though the relative contribution of absolute day length and the rate of the photoperiodic increase remains unclear. Recently, Dawson (2007) showed for the short-distance migratory European starling, *Sturnus vulgaris*, that slight seasonal changes within the range of near-equatorial photoperiods entrained precise annual rhythms of moult and gonadal growth, suggesting that these birds may respond to the shape of the annual change in photoperiod rather than to absolute day length (Dawson, 2007). Such a response mechanism could in principal operate over a wide range of latitudes, yet information on its reaction norm is lacking.

Our results clearly indicate that the photoperiodic response of the pied flycatcher to latitudinal changes in photoperiodic conditions is not linear. Even a moderate northward displacement of the wintering range from 10°N to 20°N, which is equivalent to approximately 1100 km, would result in a pronounced shift in the termination of prenuptial moult and the initiation of spring migration and gonadal growth, contradicting our previous assumption that such phenological changes would require the shift of wintering areas across a large geophysical barrier (i.e. the Sahara Desert; Coppack *et al*., 2003). However, our study also shows that a shift of the wintering area beyond this latitude would not lead to any further advancement. This

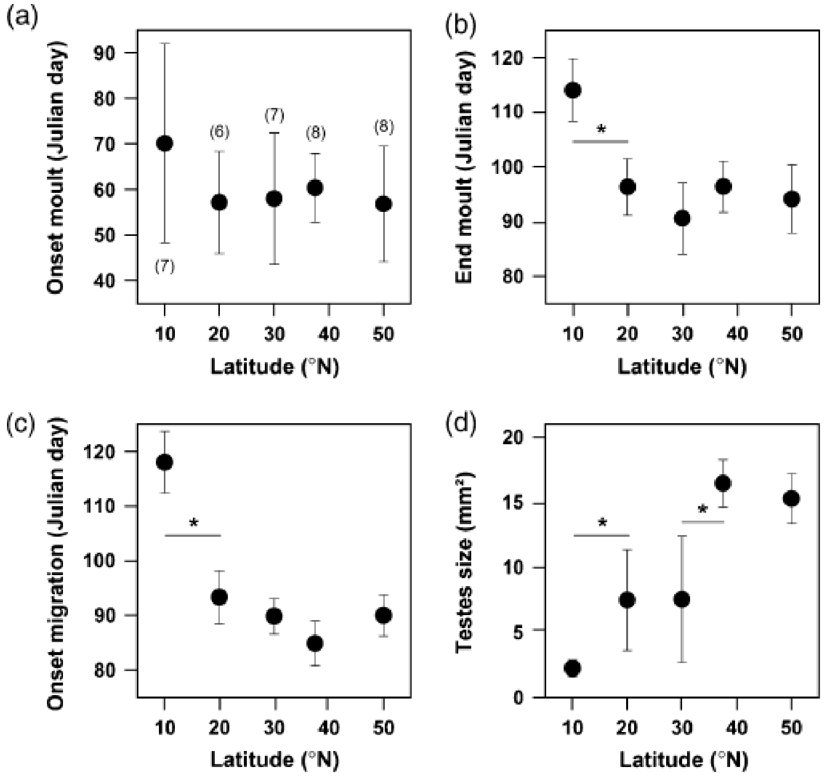

Fig. 2 Timing of (a) the onset of prenuptial moult, (b) the termination of prenuptial moult, (c) the onset of spring migration, and (d) testes size measured around April 10 (Julian day 100) in relation to experimental wintering latitude (photoperiodic treatment) in hand-raised pied flycatchers. Arithmetic means ± SD; sample sizes in parentheses; asterisks indicate significant group differences.

flattening of the reaction norm between 20°N and 50°N indicates that there may be a critical photoperiodic threshold within a narrow geographical range between 10°N and 20°N. Yet, the exact shape of the response curve, i.e. the reaction norm, within this range is currently unknown (Fig. 3).

The finding that the latitudinal shift from 10°N to 20°N elicited a pronounced advancement of moult and migration indicates that an adaptive advancement of migration and reproduction by a change in wintering area may be limited in the pied flycatcher. A shift of the current wintering areas to the north by up to 10° would involve wintering in sub-optimal habitats in the Sahel zone or at the southern edge of the Sahara Desert. Considering that desertification in this region is progressing rapidly under the influence of climate change and human activity (Newton, 2008), a successful extension or shift of the pied flycatcher's current wintering range to the north is highly unlikely. Moreover, if the photoperiodic reaction norm between 10°N and 20°N includes a critical threshold (Fig. 3a), then a change in wintering area would either result in a very strong (i.e. an advancement of migration and breeding by a month) or no response. It is unlikely that such a reaction norm would lead to adaptive changes in migration and breeding phenology, as previously suggested (Coppack *et al.*, 2003; Coppack & Pulido, 2004). Because the current wintering distribution of the pied flycatcher is restricted to a narrow band along the West African coast from the equator to approximately 15°N, it may become evolutionarily trapped by the lack of photoperiodic drive that prevents earlier departure from current wintering latitudes. However, if there is a steep but gradual response between 10°N and 20°N (Fig. 3b), then a minor shift in wintering latitude could result in a gradual advancement of migration and gonadal development, which may allow a fine tuned adjustment to rapid changes in spring phenology. Our experiment does not allow distinguishing between these two models (Fig. 3).

Future experiments should, therefore, test the capacity for adaptive photoperiodic responses on a smaller latitudinal scale than that studied here, ranging from 10°N to 20°N. Even though differences in absolute photoperiod found within this area are small, evidence is accumulating that birds can respond to the minute photoperiodic changes found close to the equator (Hau *et al.*, 1998; Dawson, 2008). In the pied flycatcher, this

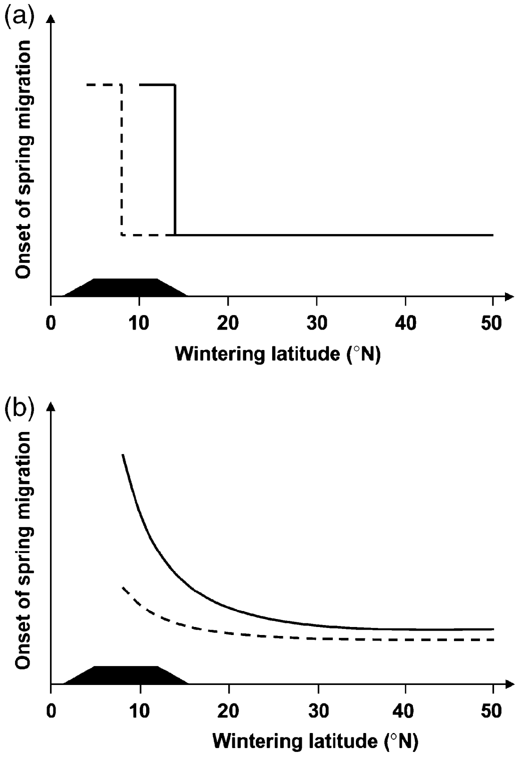

Fig. 3 Hypothetical reaction norms of the onset of spring migration in the pied flycatcher across the latitudinal photoperiodic cline inferred from experimental data (Fig. 2). The reaction norm may include a response threshold (a) or may be gradual (b). The bar on the latitude axis marks the approximate width of the pied flycatcher's current wintering range. An adaptive advancement in the onset of spring migration within this range may be accomplished by shifting the position of the response threshold (a) or by changing the slope and elevation of the reaction norm (b). Required changes in photoperiodic responsiveness are indicated by dashed lines. Models are not mutually exclusive.

range appears to be the most relevant for two reasons. First, it comprises potentially suitable wintering habitats and, therefore, shifts in wintering areas are most likely to take place within this range. Second, we find contrasting photoperiodic responses in this species that range from sustained photorefractoriness in the south (see Gwinner, 1989) to an advancement of vernal events further north (this study). The adaptive significance of this particular reaction norm might only become evident if results from the pied flycatcher are compared with photoperiodic responses of related species that differ in life history and behaviour (see Hahn & MacDougall-Shackleton, 2007). For example, collared flycatchers, *Ficedula albicollis*, which winter further south than pied flycatchers, show normal periodicity of migration and gonadal growth under conditions which are nonstimulatory for pied flycatchers (Gwinner, 1989). By comparing photoperiodic responses among species, we may be able to establish how the slope and elevation of reaction norms relate to the extent of migration. In the garden warbler, *Sylvia borin*, and the common redstart, *Phoenicurus phoenicurus*, reaction norms appear to be shallower than in the pied flycatcher (Coppack *et al.*, 2003), which may result from different selection histories associated with the use of different wintering habitats. The wintering range of the garden warbler, for example, stretches from the Sahel zone to south-eastern Africa (see Gwinner, 1996). We hypothesize that selection has favoured a gradual photoperiodic response over a wider latitudinal range in species with broader wintering ranges.

In conclusion, our results suggest that a moderate northward shift in winter range of the pied flycatcher from 10°N to 20°N may elicit a strong advancement in the onset of spring migration and gonadal maturation. Our study shows that outside this narrow range, the photoperiodic reaction norm in the timing of moult and migration is not gradual – at least not in the range of latitudes tested here. It remains unclear how this photoperiodic response is involved in the process of phenotypic adjustment to current environmental changes, and to what extent it will help long-distance migrants to keep track with rapid ongoing changes in the future. Habitat loss and deterioration in the course of increasing desertification of current and potential wintering areas may limit the potential for phenotypic advancements of spring migration and reproduction through a gradual reduction of migration distance. Thus, the rate with which long-distance migrants will be able to adapt to earlier spring conditions on the breeding grounds may strongly depend on the amount of additive genetic variation underlying extant photoperiodic reaction norms (Pulido, 2007).

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