Pied Flycatchers *Ficedula hypoleuca* travelling from Africa to breed in Europe: differential effects of winter and migration conditions on breeding date

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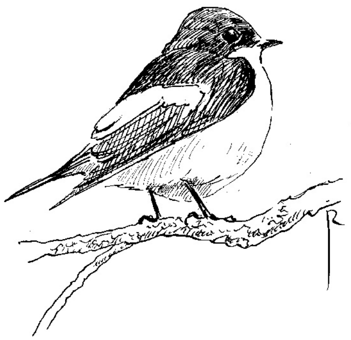

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In most bird species there is only a short time window available for optimal breeding due to variation in ecological conditions in a seasonal environment. Long-distance migrants must travel before they start breeding, and conditions at the wintering grounds and during migration may affect travelling speed and hence arrival and breeding dates. These effects are to a large extent determined by climate variables such as rainfall and temperature, and need to be identified to predict how well species can adapt to climate change. In this paper we analyse effects of vegetation growth on the wintering grounds and sites en route on the annual timing of breeding of 17 populations of Pied Flycatchers *Ficedula hypoleuca* studied between 1982–2000. Timing of breeding was largely correlated with local spring temperatures, supplemented by striking effects of African vegetation and NAO. Populations differed in the effects of vegetation growth on the wintering grounds, and on their northern African staging grounds, as well as ecological conditions in Europe as measured by the winter NAO. In general, early breeding populations (low altitude, western European populations) bred earlier in years with more vegetation in the Northern Sahel zone, as well as in Northern Africa. In contrast, late breeding populations (high altitude and northern and eastern populations) advanced their breeding dates when circumstances in Europe were more advanced (high NAO). Thus, timing of breeding in most Pied Flycatcher populations not only depends upon local circumstances, but also on conditions encountered during travelling, and these effects differ across populations dependent on the timing of travelling and breeding.

Key words: *Ficedula hypoleuca*, laying date, migration, climate

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INTRODUCTION

Long-distance migrant birds may be particularly vulnerable to climate change, because prior to departure from their wintering grounds they may lack information regarding circumstances at their breeding grounds and hence the optimal time for breeding. They may therefore have limited ability to adjust to changes in the timing of optimal breeding conditions (Both & Visser 2001, Coppack & Both 2002, Strode 2003, Both *et al.* 2006). Such species have typically evolved mechanisms to time their migration according to cues related to calendar date (Gwinner 1996, Gwinner & Helm 2003), allowing them to arrive on average at the right time on their breeding grounds. However such cues are unaltered by climate change (unlike food phenology on the breeding grounds), so that birds can arrive too late on their breeding grounds. This is especially so if they breed in habitats characterised by a short and abundant food supply when the response of the birds to such cues becomes ultimately maladaptive. The primary example of such a maladaptive response comes from a study on Pied Flycatchers *Ficedula hypoleuca*, where despite an advance of laying dates, selection for early laying has continued to strengthen, but the spring arrival dates of birds have not advanced (Both & Visser 2001, Hüppop & Winkel 2006). These flycatchers have advanced laying dates by reducing the interval between arrival and the start of egg-laying, but the extent of this adjustment is ultimately constrained by the date of arrival.

Contrary to the argument that long-distance migrants are absolutely constrained in their arrival time to adjust to climate change, several European species show clear advances in spring arrival in recent decades (Hüppop & Hüppop 2003, Cotton 2003, Sokolov & Kosarev 2003, Sokolov L.V. 2000, Huin & Sparks 1998, Huin & Sparks 2000, Lehikoinen *et al.* 2004, Sparks 1999, Jonzen *et al.* 2006) and North America (Marra *et al.* 2005, Butler 2003, Bradley *et al.* 1999). Spring arrival of long-distance migrants appears more flexible than expected, showing correlation with factors during migration (Huin & Sparks 1998, Huin & Sparks 2000, Hüppop & Hüppop 2003, Sokolov 2000, Marra *et al.* 2005, Hüppop & Winkel 2006, Both *et al.* 2005) or on the wintering grounds (Saino *et al.* 2004, Cotton 2003, Sokolov & Kosarev 2003), opening up the possibility that birds can adjust timing of migration to climate change. In addition, for Pied Flycatchers there is now evidence that spring arrival has advanced at some sites (Hüppop & Hüppop 2003, Sokolov 2000) but not in others (Hüppop & Winkel 2006), and that it is correlated with environmental circumstances during migration (Hüppop & Hüppop 2003, Ahola *et al.* 2004, Both *et al.* 2005). The observed correlation between arrival and environmental circumstances encountered en route has been used to challenge the idea that inflexible migration schedules constrain any adaptive adjustment to climate change (Marra *et al.* 2005, Jonzen *et al.* 2006). It is this notion that we want to address in this paper.

If spring arrival constrains breeding date, we might expect individual breeding dates to correlate with arrival dates as found in Pied Flycatchers (Alatalo *et al.* 1984, Potti & Montalvo 1991) and other species (Smith & Moore 2005, Bensch & Hasselquist 1992, Cristol 1995). More indirectly, we also expect a correlation between environmental circumstances *en route* and breeding date, because these circumstances probably affect speed of migration and hence arrival date, which in turn determines breeding date (Both *et al.* 2005, Hüppop & Winkel 2006). It may be that environmental circumstances at the wintering grounds also have an effect, because these may allow birds to initiate their migration earlier. The effects on breeding dates of environmental conditions at the wintering grounds and during migration may thus be key to understanding how severely long-distance migrants are constrained by their migration in adjusting to climate change.

In this paper, we address the following questions: (1) Are environmental circumstances at the wintering grounds or during migration correlated with the advance of spring at the breeding areas, and are birds on the wintering grounds therefore able to predict when they should arrive at the breeding grounds? (2) Are there effects of environmental circumstances at the wintering grounds, or during migration, on the timing of laying in different populations of Pied Flycatchers across Europe? For these purposes we used data on annual laying dates from 17 long-term populations of Pied Flycatchers for which some have advanced as a result of climate change, while others have not (Both *et al.* 2004). The extent of advance was correlated with the extent of spring warming at each locality, and here we investigate whether on top of these local temperature effects, laying dates were correlated with environmental circumstances during wintering and migration.

METHODS

We used 17 long-term population studies of nest box breeding Pied Flycatchers in the period 1982–2000 when vegetation indices (NDVI, see below) were available (Both *et al.* 2004). Populations with less than 16 years of data were excluded, as were Collared Flycatcher *Ficedula albicollis* populations because of their different winter distribution. At study sites nest boxes were checked weekly in most instances, and the laying date of each nest was calculated assuming that one egg was laid every day. Where laying date could not be determined this way, but hatch date was known, we assumed 13 days for incubation (beginning on the last egg) and that one egg was laid per day. For each year and study site combination, we calculated the median laying date. Only first broods were included, which excluded broods of females that were previously known to have started a brood in that year, as well as broods that were started later than 30 days after the very first brood in that year for each study site. The first year of nest box provisioning at each study site was excluded from the analyses, because newly established populations contain a high proportion of young birds that tend to lay later in the season (Lundberg & Alatalo 1992).

Study sites covered most of the species' breeding range, from Spain in the south to Northern Finland in the north, and from Wales in the west to Moscow in the east. Study sites were not spread evenly over Europe because we used existing datasets collected for other purposes. Daily mean temperatures were obtained from meteorological stations close to the study sites. Populations at different latitudes commencing breeding on different dates, and are therefore expected to respond to temperatures at different times in the year. To assign a time window to calculate site specific temperatures we calculated the mean of the annual median laying dates of the first five years for each study area (1982–1986 for all areas except La Hiruela, which was 1985–1989). Mean daily temperatures from the 30 day period before this date were taken as the local temperature effect (see Both *et al.* 2004 for rationale). Average laying date for each population was calculated for 1985–1989. This restricted period was used because laying date advanced strongly in some populations in response to local increases in spring temperature since 1980, while others did not (Both *et al.* 2004).

Environmental variables

Timing of migration and consequently timing of breeding may be affected by conditions the birds encounter on the wintering grounds and during migration. Pied Flycatchers winter in west-Africa, mainly in the Sahel area (Lundberg & Alatalo 1992), and have to cross the Sahara en route to the European breeding areas. For some areas in Africa (Fig. 1), the Normalized Difference Vegetation Index (NDVI) based on satellite images was calculated. This index is calculated as the normalized difference in reflectance between red (0.55–0.68 μm) and infrared (0.73–1.1 μm) channels of the Advanced Very High Resolution Radiometer (AVHRR) sensor of National Oceanic and Atmospheric Administration (NOAA) satellites and processed by the National Aeronautics and Space Administration (NASA, Prince & Justice 1991a). NDVI provides a measure of the amount and vigour of vegetation at the land surface related to the level of photosynthetic activity (Prince & Justice 1991b, Myneni *et al.* 1997). This index is strongly correlated with the fraction of photosynthetically active radiation absorbed by vegetation, which depends on local rainfall conditions (Asrar *et al.* 1984, Myneni *et al.* 1995). Since Pied Flycatchers are insectivorous and the insect abundance in turn depends on plant productivity, the NDVI is likely to reflect the relative seasonal abundance of insect supplies in the wintering areas (Szép & Møller 2005, Wolda 1988, Dean & Milton 2001). NDVI data corrected for surface topography, land-cover type, presence of clouds and solar zenith angle were provided by Clark Labs in IDRISI format as world monthly images at spatial resolutions of 0.1 degree from a 0 to 255 scale values between August 1981 and December 2000 (excepting September-December 1994). Using a Geographic Information System (Clark Labs 2001), we obtained mean NDVI values for those selected areas in Africa (see Fig. 1) from December to April.

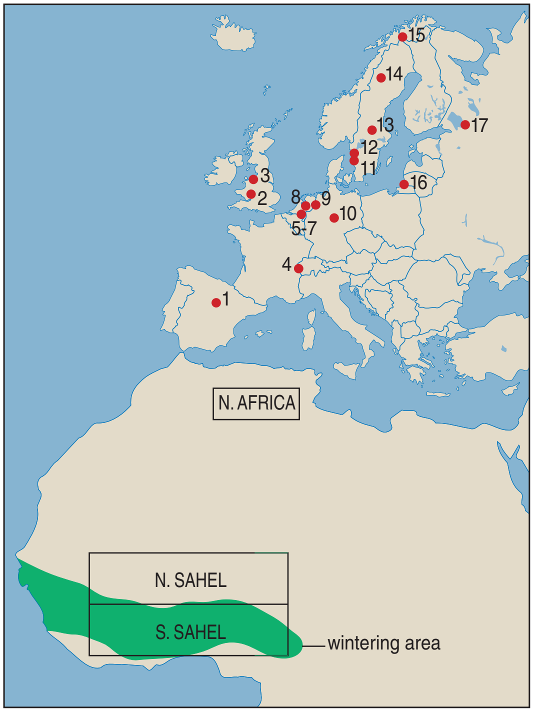

Figure 1. Map indicating areas used for NDVI data extraction and sites of population studies of Pied Flycatchers in Europe.

A second environmental variable analysed was the North Atlantic Oscillation (NAO). NAO is a natural large scale atmospheric fluctuation

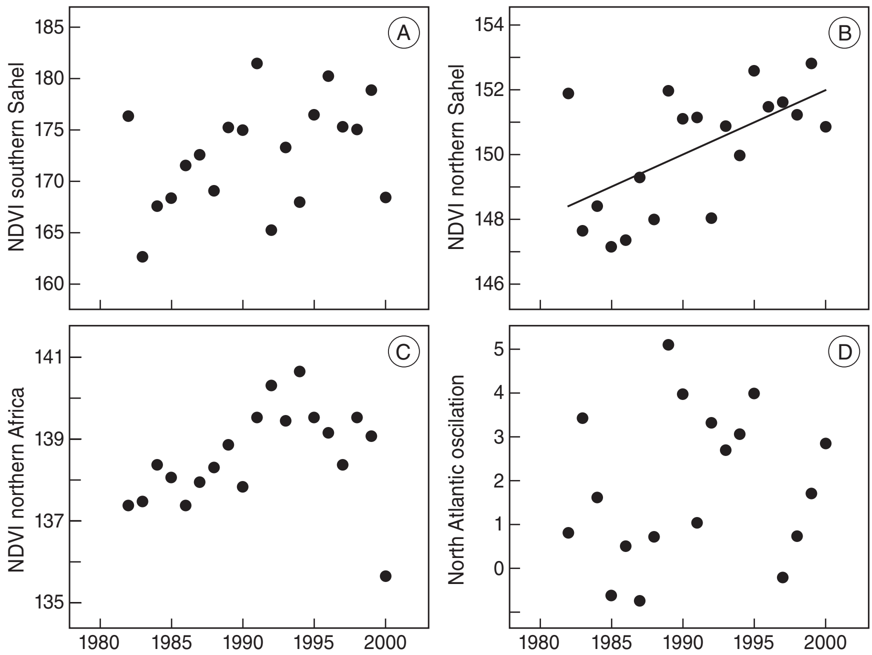

Figure 2. Annual values of NDVI in the different areas in Africa as used in the analysis and winter NAO (Dec–Mar).

between the subtropical (centred on the Azores) and the subpolar (centred on Iceland) North Atlantic region (Lamb & Peppler 1987). This phenomenon is particularly important in winter, when it exerts a strong control on the climate of Europe and when it exhibits the strongest interdecadal variability (Hurrell 1995). The NAO-index is quantified from December to March as the difference of normalized sea level surface pressures between Lisbon, Portugal and Stykkisholmur/ Reykjavik, Iceland from 1864 through 1998 (Hurrell & VanLoon 1997). This winter NAO-index is currently updated at the website: http://www.cgd.ucar.edu/~jhurrell/nao.html. The winter NAO-index can be either positive or negative, and major climate variations occur when it remains for long periods in one mode or in the other (Hurrell 1995). A positive NAO-index results from intensifying high pressure over the subtropical Atlantic and deepening low pressure over the subpolar Atlantic, and is associated with stronger, more southerly tracking of westerly winds and higher temperatures in western Europe. A negative NAO occurs when the subtropical Atlantic high pressure is weak and the subpolar Atlantic low pressure moves south, associated with cold drier winter in northern Europe and wetter winters in southern Europe.

RESULTS

Temporal trends in environmental variables

Temporal trends in local temperatures in the different breeding areas have been described before, and these differ geographically, with strong increases in western and central Europe and only mild or no increases in southern, northern and eastern Europe (see Both *et al.* 2004 for details). Among the NDVI data from Africa we found an increase over the years in the northern Sahel zone ($r = 0.60$, $n = 19$, $P = 0.007$, Fig. 2), and no sig-

Table 1. Details of the population studies of Pied Flycatchers, the correlation between local spring temperature and NDVI index in different parts of Africa and NAO, and the possible maximal effect sizes of the different environmental variables on laying date (LD) for these populations. Significant correlations are in bold. Population identifiers in first column refer to Fig. 1.

						LD	Correlation between local temp and				Maximal possible effect sizes on laying date of				
No.	Area	Latitude	Longitude	First	Last	1985–1989	S Sah	N Sah	N Afr	NAO	Local temp	S Sah NDVI	N Sah NDVI	N Afr NDVI	NAO
1	La Hiruela	41°04'N	03°27'W	1985	2000	23 May	–0.36	0.09	0.11	0.42	–8.37	–6.42	5.15	2.91	–4.52
2	Llanwrthwl, Powys	52°13'N	03°27'W	1982	2000	13 May	–0.13	0.16	–0.11	0.24	–4.70	–8.16	3.19	0.44	–9.25
3	Abergwyngregyn	53°13'N	04°00'W	1982	2000	12 May	–0.28	0.02	0.04	0.18	–3.55	8.57	–9.74	–1.57	–1.10
4	Baulmes	46°47'N	06°31'E	1982	2000	18 May	–0.25	0.06	–0.04	0.15	–8.94	9.19	–8.89	6.04	0.38
5	Hoge Veluwe	52°02'N	05°51'E	1982	2000	13 May	–0.21	0.06	–0.18	0.17	–7.91	13.23	–9.30	–1.72	5.34
6	Warnsborn	52°00'N	05°51'E	1982	2000	13 May	–0.12	0.14	–0.15	0.23	–6.65	9.23	–7.01	–4.75	2.45
7	Deelerwoud	52°05'N	05°55'E	1982	2000	12 May	–0.12	0.14	–0.15	0.23	–6.65	12.02	–6.75	–0.01	3.40
8	Staphorst	52°37'N	06°17'E	1982	2000	11 May	–0.13	0.12	–0.18	0.20	–6.65	11.87	–7.43	–2.58	7.10
9	Lingen/Emsland	52°27'N	07°15'E	1982	2000	14 May	–0.32	–0.04	–0.24	0.21	–9.74	8.44	–6.91	–2.89	7.50
10	Harz	51°53'N	10°37'E	1982	2000	16 May	–0.33	0.02	–0.27	0.26	–11.69	–2.17	1.65	–0.14	–4.46
11	Gunnebo	57°40'N	12°05'E	1982	1998	25 May	**–0.51**	–0.43	0.03	0.35	–6.88	16.11	–11.26	8.17	–1.85
12	Goteborg	57°43'N	11°58'E	1982	2000	26 May	–0.29	–0.05	0.00	0.38	–6.42	–3.18	0.81	–1.17	–4.81
13	Borlange	60°23'N	15°30'E	1982	1999	27 May	–0.40	–0.30	0.15	**0.49**	–6.53	15.22	–9.67	8.66	1.91
14	Ammarnäs	65°58'N	16°13'E	1982	2000	8 Jun	**–0.59**	**–0.49**	–0.17	0.32	–6.65	6.01	1.39	7.53	–1.73
15	Kilpisjärvi	69°03'N	20°50'E	1982	2000	10 Jun	**–0.46**	–0.44	–0.21	0.24	–6.76	–1.11	8.72	5.09	–7.72
16	Rybachy	55°05'N	20°44'E	1982	2000	28 May	**–0.48**	**–0.57**	–0.34	0.04	–4.13	10.51	–5.83	2.74	–4.10
17	Karelia	60°46'N	32°48'E	1982	2000	30 May	–0.31	–0.30	0.07	0.24	–7.11	1.36	2.20	3.80	–8.27

nificant changes in the southern Sahel zone (r = 0.37, n = 19, P = 0.110), nor in northern Africa (r = 0.28, n = 19, P = 0.250). However, these temporal trends were not significantly different across areas, and the non-significant effects are to a large extent determined by the extreme last year (see Fig. 2). Excluding this year yields significant correlations between NDVI and year for all three areas (northern Sahel r = 0.61, P < 0.001, southern Sahel: r = 0.50, P = 0.040, northern Africa: P = 0.68, P = 0.002, n = 18). NAO was not correlated with year for this period of time (r = –0.022, n = 19, P = 0.99).

Correlations between environmental variables

Across areas there was a strong correlation between NDVI in the southern and northern Sahel (r = 0.78, n = 19, P < 0.001), but not between the Sahel and northern Africa nor with NAO (all r < 0.21, all P > 0.390). It therefore seems that the vegetation experienced by the flycatchers south of the Sahara does not provide them with information regarding what they can expect later in their journey in northern Africa or in Europe in general (as exemplified by NAO).

If correlations exist between environmental conditions at the wintering grounds and in the local breeding area, birds may have evolved to use such cues to start spring migration. Therefore, we examined correlations between vegetation in Africa and NAO and the spring temperatures at the 17 breeding localities (Table 1). Only in a few cases were significant correlations found between NDVI in the Sahel zone or NAO and spring temperatures in Europe, and these few correlations could be due to chance effects. However, we examined whether there were any patterns in the correlation coefficients between European spring temperatures and African NDVI across breeding localities, and we found that areas which have a late laying date showed a stronger correlation between NDVI in the Sahel and local spring temperature. We found no such correlation in areas with an early laying date. In the late laying areas, more vegetation in the Sahel coincided with low temperatures in the breeding areas (Fig. 3).

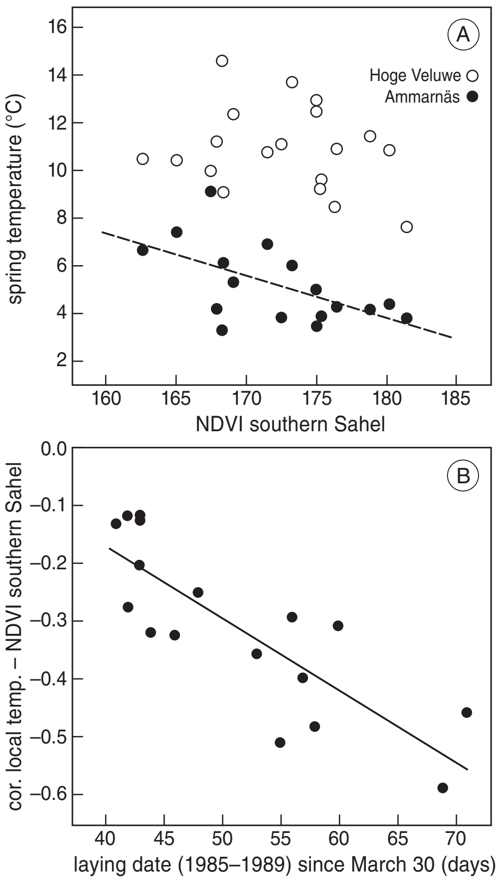

Figure 3. Correlations between vegetation in the southern Sahel and local spring temperatures at different breeding localities in Europe. (A) Two examples of areas of how these variables are correlated. (B) Per area the correlation coefficient and its relation to the average laying date in each area (correlation: r = 0.82, n = 17, P < 0.001).

Flycatchers from more northern and eastern populations may thus use the lack of rainfall related vegetation on the wintering grounds to advance their migration, because in those years it is more likely that spring starts earlier.

Breeding date and environmental conditions

The annual median laying date advanced clearly with rising local temperatures, and did not differ across populations (Table 2). Additionally, laying

Table 2. Results of ANCOVA on annual median breeding date of 17 populations of Pied Flycatchers in relation to local temperatures and environmental conditions on the wintering grounds and during migration. Slopes are given for main effects.

Dependent variable	*df*	*F*	*P*	Slope (SE)
Intercept	1,225	23.72	< 0.0005	
Breeding area	16,225	3.10	n.a.	
Local temperature	1,225	95.08	< 0.0005	–1.180 (0.120)
Year	1,225	14.35	< 0.0005	–0.156 (0.043)
NDVI southern Sahel	1,225	21.38	n.a.	
NDVI southern Sahel	1,225	9.42	n.a.	
NDVI northern Africa	1,225	6.18	n.a.	
NAO	1,225	1.59	n.a.	
Breeding area x NDVI southern Sahel	16,225	2.27	0.004	
Breeding area x NDVI northern Sahel	16,225	2.68	0.001	
Breeding area x NDVI northern Africa	16,225	2.19	0.006	
Breeding Area x NAO	16,225	2.30	0.004	
Non-significant terms				
Breeding area x Local temperature	16,209	1.13	0.33	
Breeding area x Year	16,193	1.57	0.08	

date advanced by three days, and again this was not different across populations. In contrast, the effects of NDVI in both the southern and northern Sahel, and northern Africa, as well as NAO, differed significantly between populations (Table 2). Some examples of the effects of all four environmental factors are given in Fig. 4, showing different relationships between laying dates of Pied Flycatchers in different populations and NDVI in different parts of Africa and NAO.

The different effects of environmental circumstances at the wintering grounds or during migration are not random, but depend on the average laying date of each population (Fig. 5). MANOVA on the slopes of southern Sahel NDVI, northern Sahel NDVI, northern African NDVI and NAO against breeding date (see model in Table 2) showed a significant effect of average laying date (Wilks' lambda = 0.173, $P < 0.001$). More specifically, in populations with an early laying date, more vegetation in both the northern Sahel and northern Africa was associated with an advance in laying date (simultaneously taking local temperature into account, Fig. 5B,C), whereas in late breeding populations the vegetation in northern Africa was associated with a delayed effect on laying date (Fig. 5C). The opposite was the case for the associations with NAO: in years with a relatively mild and wet winter (high values of NAO) the flycatchers delayed laying in areas with a early laying date, whereas in areas with an late laying date these conditions advanced the laying date (Fig. 5D). The effects of northern African NDVI and NAO were on average smaller for these early breeding populations, and stronger for late breeding populations.

What do these different environmental effects mean quantitatively for laying date in different areas? For this purpose, we calculated the magnitude of the effects for all variables using the study area specific slopes for the different environmental effects from the model in Table 2. Next we calculated how laying date changed from the minimal

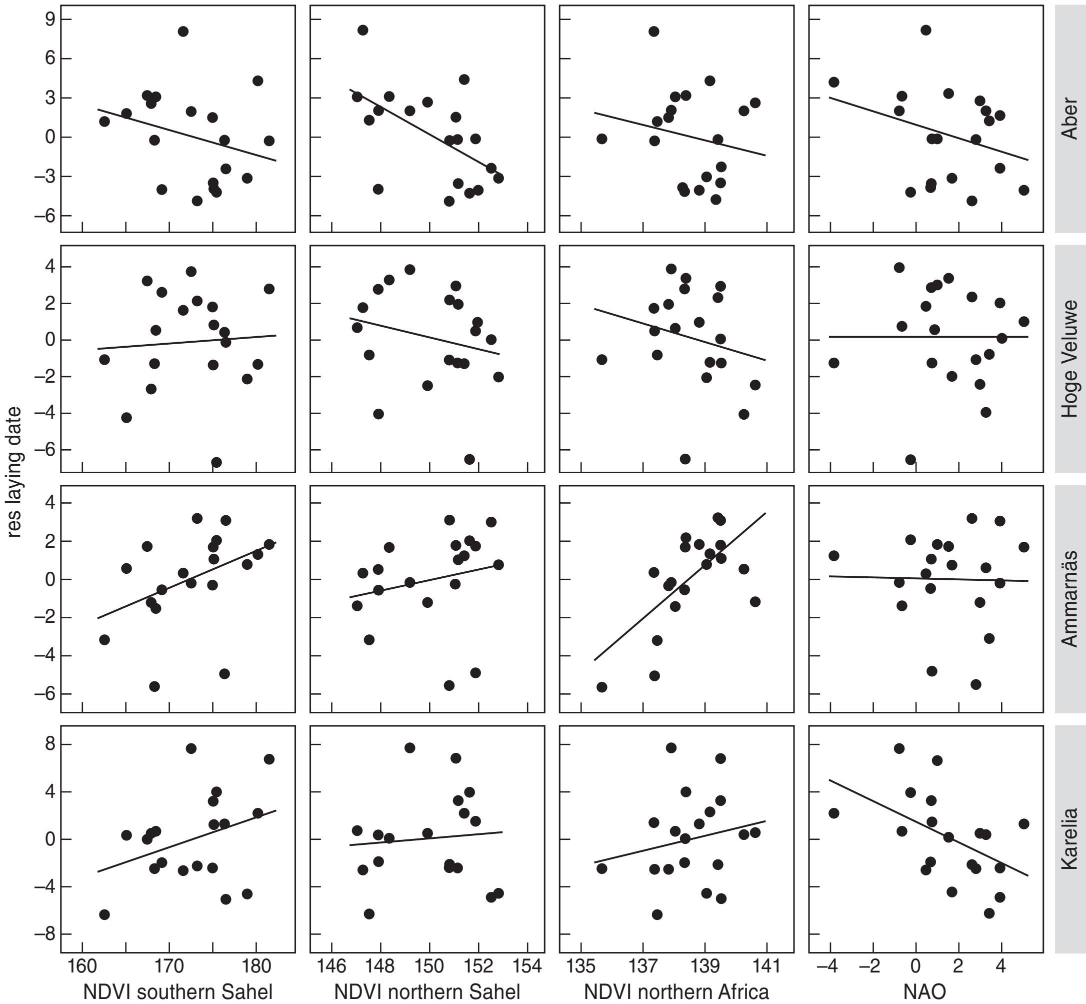

Figure 4. Effects of the vegetation index (NDVI) in three parts of Africa and NAO on the laying dates of four Pied Flycatcher populations. On the y-axis the residual laying date is given from a model including only local spring temperature. The rows are different populations: from top to bottom: Abergwyngregyn (Wales), Hoge Veluwe (Netherlands), Ammernäs (Sweden), Karelia (Russia). The different columns are for effects of different environmental variables: NDVI southern Sahel, NDVI northern Sahel, NDVI northern Africa, NAO.

to maximal value for each environmental factor (Table 1, assuming that all of these were independent). The maximal magnitudes of each environmental factor on laying date depended thus on the variation in the factor, as well as on the study area specific slope of the factor on laying date. Because areas did not differ in the effect of local spring temperature, it is not surprising that increases in spring temperature always advanced laying date. The effects of vegetation in the two Sahel areas were more complicated, because annual NDVI values are highly correlated across the southern and northern Sahel, and so for each population the effect of northern Sahel NDVI tends to be opposite

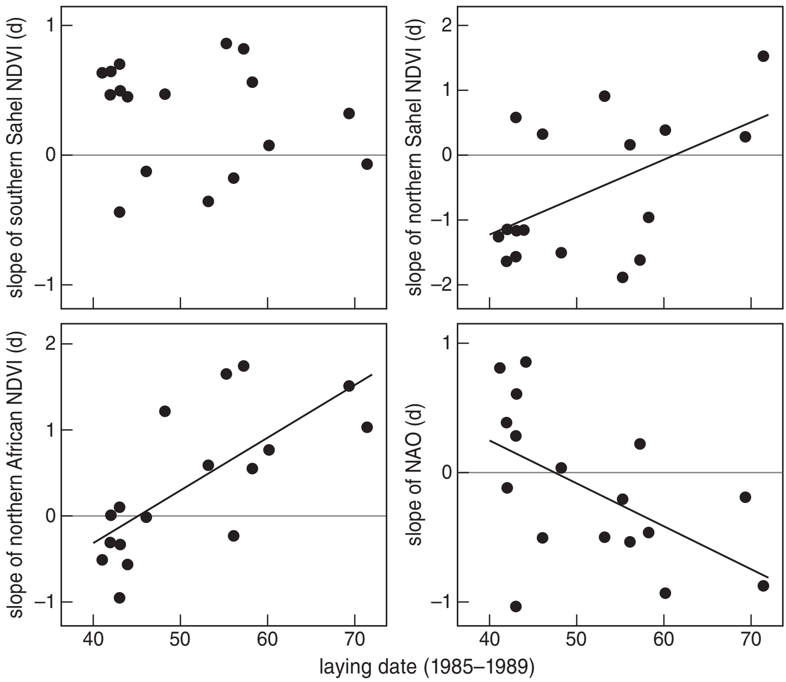

Figure 5. The strength of the effect of different environmental variables on laying date in different populations of Pied Flycatchers in relation to the average laying date of these populations. Each data point represents one study area and is the area specific slope of laying date and the environmental variable. For NDVI positive values mean that more vegetation delays laying date. For NAO positive values mean that laying date advances after a relatively mild winter. The univariate effects are: southern Sahel: $F_{1,15}$ = 0.54, P = 0.470, northern Sahel: $F_{1,15}$ = 5.54, P = 0.030, northern Africa: $F_{1,15}$ = 15.63, P = 0.001, NAO: $F_{1,15}$ = 5.87, P = 0.030.

to the effect of southern Sahel NDVI (correlation between slopes of laying date to either southern or northern Sahel NDVI: r = –0.88, n = 17, P < 0.001). Thus, on average, an increase in vegetation in the southern Sahel had a delaying effect on laying date in most populations, but this is mostly balanced by the advancing effect of vegetation in the northern Sahel. This does not mean that these effects of Sahel vegetation are therefore non-existent. For example, in the Hoge Veluwe area we depicted the effects of the variation in the two NDVI-indices, and this example shows that with the same vegetation in the southern Sahel there is a potential variation of eight-days in laying date, whereas a variation of nine days is possible for the same value in the northern Sahel NDVI (Fig. 6).

DISCUSSION

Predicting breeding conditions at wintering or migration sites

If there is a correlation between climatic conditions at the wintering site and the breeding site, birds may use the information at the wintering site to adjust the timing of migration in order to arrive at the right time at the breeding grounds. We found no correlations between the rainfall related vegetation development in the Sahel zone and the spring temperature at the breeding grounds in populations breeding early, but for late breeding populations we found that dry years in the southern Sahel coincided with warm springs at the breeding grounds. Flycatchers in these populations

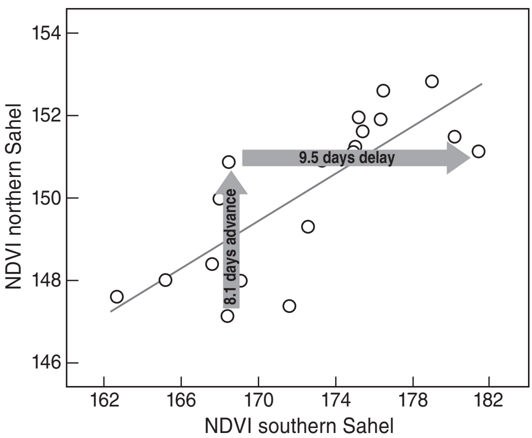

Figure 6. The correlation between the vegetation index in the southern and northern Sahel across different years, and as example we depict here the effect variation in vegetation in both areas can have on variation in laying date in the Hoge Veluwe area. Along the regression slope the effect of variation in both vegetation indices is only small (i.e. a four-day delay from the bottom-left to the top-right corner).

would therefore benefit from starting earlier migration in dry years in order to arrive favourably early at the breeding grounds.

In addition, environmental circumstances during migration may provide birds with information regarding the advance of the spring at their breeding grounds. However, we found few correlations between either northern Africa NDVI or NAO and spring temperatures at the breeding grounds. Not surprisingly, correlations with NAO were all positive (although only one was significant), reflecting the effect of the prevailing winds on temperatures in large parts of Europe. Birds can of course not measure NAO directly, but since its effect probably leads to an advance of spring in large parts of Europe, its effects may give some information on the advance at each breeding locality, even given the low correlation coefficients involved.

Conditions at the wintering grounds and breeding date

We have found that populations differed in the effect of vegetation in sub-Saharan Africa on laying dates. These effects of vegetation development in the wintering areas on laying date are difficult to interpret from our correlations. In breeding populations with a positive effect from the northern Sahel on laying date we found a negative effect from the southern Sahel and *vice versa*. Moreover, the annual NDVIs in both areas were highly correlated, and the positive effect from one area on laying date was on average counterbalanced by the negative effect from the other area. This does not mean that the effects may be trivial, and in Fig. 6 we illustrate that with the variation that exists across the northern and southern Sahel NDVI the laying date may be either advanced or delayed considerably. It is difficult to understand why within some populations the southern Sahel vegetation tends to advance laying, and northern Sahel vegetation tends to delay it, whilst in others these effects are completely reversed, but this may result from breeding populations wintering at different sites. If so, we might have expected clearer results showing geographically close breeding populations with similar pattern, or a correlation of this effect with the average laying date of populations, but neither were found. Since it is difficult to give a biological explanation to the correlations between sub-Saharan vegetation and laying dates, we cannot conclude whether there is any real effect of environmental circumstances in the wintering grounds on the breeding dates in Europe.

Recently, some studies have reported correlations between arrival date at the breeding grounds and environmental conditions at the wintering grounds (Saino *et al.* 2004, Cotton 2003, Sokolov & Kosarev 2003), suggesting that birds not only time their migration to internal or day-length related clocks (Gwinner 1996, Gwinner & Helm 2003), but also to environmental conditions. These internal clocks induce physiological changes in the birds, preparing them for the start of migration, and constraining how early birds can migrate. The environmental conditions at the time the birds start their internal migratory program may therefore modulate the actual timing of migration. Under favourable environmental conditions, the interval between the internally based start of the migration program and the actual start of migration may be small, while in adverse circumstances this interval may become larger. In such a model, the start of migration is constrained by an internal clock, only if circumstances at the wintering sites are favourable. Whether environmental conditions at the wintering grounds influence arrival and breeding dates therefore depends upon how often environmental conditions constrain the actual start of migration, and whether the speed of migration is related to environmental conditions *en route*, and this may make it difficult to detect these type of effects on the breeding grounds.

Conditions during migration and breeding date

We have shown that Pied Flycatchers breed earlier when it was warmer at their breeding locality, and that environmental circumstances *en route* have an additional effect, but this effect differed between populations. Early breeding populations advanced their laying date with more vegetation in Northern Africa (probably wet conditions). In late breeding populations the effects were more pronounced, with an advance in laying date with low vegetation index in Northern Africa (probably dry circumstances) and a relatively mild winter (high NAO) in Europe. In the discussion below we assume that annual variation in NDVI in Africa is to a large extent related to variation in rainfall (Schmidt & Karnieli 2000), and insect availability relies on vegetation growth (Wolda 1988, Dean & Milton 2001).

In general one would expect that more (rainfall related) vegetation in Northern Africa would make circumstances for migration easier and hence advance arrival and breeding (Møller & Merilä 2004), but this was only found amongst early breeding populations while late breeding populations advanced breeding with dry conditions. The timing of passage through northern Africa of late breeding populations is probably later than earlier breeding populations (Bell 1996), so the degree to which rainfall may create favourable circumstances may change during the season. Thus, early in the migration season rainfall may improve circumstances for breeders because they profit from the explosion in insect emergence following the rain. However, in such years the insects may be gone by the time the late populations pass by, and therefore late populations may in fact profit from dry circumstances when at least some limited amount of food is available. The profitability of particular environmental circumstances may thus depend to a large extent on time and place, and populations of the same species of different geographical origin may be affected differently by the same environmental factors.

The North Atlantic Oscillation affects the nature of the weather in large parts of Europe, and can therefore be considered as a good indicator of the environmental conditions encountered during the second part of migration. The effect of NAO again showed differences across populations: in early breeding populations there was, on average, little effect of NAO on the timing of breeding, while late populations advanced when winters and spring were mild (high values of NAO). This lack of an effect in early populations may be because they migrate generally shorter distances through Europe, and may therefore be less affected by environmental circumstances. That late breeding populations can advance as a result of high NAO values has been shown before: the timing of passage on Helgoland of migrants heading for Scandinavia has been shown to advance in years with high NAO values (Hüppop & Hüppop 2003). Under these circumstances birds can probably speed up their migration, because of more favourable circumstances *en route* to refuel (Jenni & Schaub 2003, Schaub & Jenni 2001). In an earlier study on breeding dates of Pied Flycatchers across Europe, it was also found that NAO had a stronger effect on more northern populations (Sanz 2003), even without taking local spring temperatures into account. We suggest that the NAO effects reported here are not so much an effect of local breeding circumstances, but rather are an effect of circumstances encountered during migration.

Travelling to breed: are breeding dates constrained by arrival?

In this study we have looked at patterns of environmental conditions on the wintering grounds and during migration on breeding dates in 17 populations of Pied Flycatchers. The effects of wintering conditions were difficult to interpret, but we found clear effects of circumstances during migration on breeding dates, although these differed across populations. There are two non-exclusive hypotheses why birds breed earlier if circumstances *en route* are more favourable: (1) they migrate at higher speeds because they can refuel more quickly and therefore arrive earlier, or (2) they arrive in better condition and therefore they can reduce the time between arrival and the start of breeding. Pied Flycatchers show reverse migration under adverse spring circumstances (Walther & Bingman 1984), and refuelling rates have been found to be higher under more favourable conditions (Bairlein & Hüppop 2004, Jenni & Schaub 2003, Schaub & Jenni 2001), thereby supporting the first hypothesis. Additionally, there are several studies showing that within years the early arriving birds also lay early, supporting the idea that arrival date indeed constrains laying (Smith & Moore 2005, Cristol 1995), and that across years late arrival leads to reduced pre-laying intervals (Potti 1999). There is some evidence against the second hypothesis, because within years there is no relationship between the interval between arrival and breeding and female condition (Potti 1999, Smith & Moore 2005), and Pied Flycatchers on average arrive with low body reserves at their breeding grounds (Silverin 1980). Conditions during migration therefore most likely affect arrival date, which in turn affects breeding dates.

The finding that arrival date is to a certain extent determined by environmental circumstances *en route*, has been used to question the hypothesis that relatively inflexible migration schedules constrain species in their adjustment to climate change (Marra *et al.* 2005). The reasoning is that if arrival date is advanced under favourable climatic conditions, arrival cannot be such a constraint in advancing breeding date under climate change. Although arrival is not as inflexible as we may have suggested earlier (Both & Visser 2001), it may still be the case that the 'optimal breeding time' is advancing faster than the birds' arrival time, and hence the average breeding date. Furthermore, our data showing that breeding dates do simultaneously correlate with local spring temperatures, as well as with vegetation in North Africa, suggests that breeding dates are to a certain extent constrained by arrival time and/or condition at arrival (either of which may depend on circumstances *en route*). As the start of the migratory process is likely to depend to some extent upon day-length or internal clocks (Gwinner 1996, Gwinner & Helm 2003), even an improvement in conditions on the wintering grounds is likely to be constrained in its effects on the start of migration. Because birds apparently lay earlier when they arrive earlier, and since advancing arrival must be constrained by internal programs determining the start of the migration program, it is most likely that adjusting laying date to climate change must be constrained by such a migration program. This is despite the fact that, as we have shown here, environmental variation in conditions at both the wintering grounds and during migration speed up migration.

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SAMENVATTING

Veel vogelsoorten hebben een korte periode beschikbaar om te broeden, omdat de omstandigheden in hun leefomgeving door seizoensinvloeden sterk veranderen. Wanneer vogels broeden, hangt onder meer af van het moment van aankomst in het broedgebied, die – zeker bij langeafstandstrekkers – bepaald wordt door de treksnelheid. De treksnelheid is afhankelijk van de omstandigheden in het overwinteringsgebied en gedurende de trek; factoren als temperatuur en de hoeveelheid regen kunnen hierbij belangrijk zijn. Kennis omtrent deze cruciale factoren zou het mogelijk kunnen maken te voorspellen hoe goed soorten zich aanpassen aan klimaatsveranderingen. Dit artikel geeft een analyse van effecten van vegetatiegroei in het overwinteringsgebied en langs de trekroute op het tijdstip van broeden van 17 populaties Bonte Vliegenvanger *Ficedula hypoleuca* in de periode 1982–2000. Het tijdstip van broeden was niet alleen nauw gecorreleerd met de voorjaarstemperatuur in het broedgebied, maar ook met de vegetatiegroei in Afrika en met de NAO (North Atlantic Oscillation, een maat voor variatie in luchtdruk over de Atlantische Oceaan en grote delen van Europa). De effecten van vegetatiegroei in het overwinteringsgebied en langs de trekroute verschilden tussen populaties. Datzelfde gold voor de omstandigheden in Europa zoals gemeten door middel van de winter NAO. In het algemeen broedden de vroege populaties van het laagland en in West-Europa eerder in jaren met meer vegetatiegroei in de Noordelijke Sahel en Noord-Afrika. Daarentegen kwamen late populaties uit het hooggebergte en uit Noord- en Oost-Europa eerder tot broeden in jaren met een vroege zomer (samenvallend met een hoge NAO). De effecten verschillen dus tussen populaties afhankelijk van wanneer precies de vliegenvangers trekken en broeden.

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