



# Patterns of spring arrival dates differ in two hirundines

Tim Sparks<sup>1,\*</sup>, Piotr Tryjanowski<sup>2</sup>

<sup>1</sup>NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK

<sup>2</sup>Department of Behavioural Ecology, Adam Mickiewicz University, Umultowska 89, 61 614 Poznań, Poland

**ABSTRACT:** We examined the first arrival dates in the UK over a 56 yr period of 2 hirundines, sand martin *Riparia riparia* and barn swallow *Hirundo rustica*, in relation to temperatures along migration routes and at destination. Changes in arrival dates have been much greater for sand martin than for barn swallow, and the arrival order of the 2 species now appears to have reversed. There appear to be 2 reasons for this: a greater response to temperatures in SW Europe and a different response to temperature in recent years, leading to earlier arrival at the same temperature than formerly. We argue that this may involve evolutionary change, but conclude that it is difficult to be definite about this without information on individual animals.

**KEY WORDS:** Bird migration · Phenology · Barn swallow · Sand martin · Plasticity · Adaptation · Temperature response

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## 1. INTRODUCTION

Many migratory bird species are changing their behaviour in response to a warming climate. Findings have included a change from migratory behaviour to residency, an expansion to higher latitude wintering areas and, in particular, a tendency to earlier arrival in spring (Lehikoinen et al. 2004). The meta-analysis of Lehikoinen et al. (2004) suggested that 40% of approximately 1000 bird series had become significantly earlier in spring arrival dates in the second half of the 20th century, while only 2% had become significantly later. Reported changes to migration phenology are increasing in the scientific literature. However, it appears that changes in migration phenology are not, in general, matching the reported advances in phenology of plant and invertebrate species on which the migrants may rely (e.g. Peñuelas et al. 2002). This raises concerns of phenological mismatching in food webs, although it is anticipated that selection in birds, i.e. evolutionary change, may, in time, rectify the situation (Pulido & Berthold 2004). As future changes in temperature are likely to be rapid (IPCC 2007), an adequate response to temperature may be crucial and under strong evolutionary pressure. Unless there is

rapid adaptation in birds to match changes in invertebrates, reductions in breeding output and perhaps population levels may result (Both et al. 2006).

Of the changes so far experienced, can we detect evidence of evolutionary change? Are we able to distinguish between changes resulting merely from phenological plasticity, individual learning and genetically controlled evolution? Two recent papers (Bradshaw & Holzapfel 2006, Jonzén et al. 2006) make claims of evolutionary change, but, unless the identity and family history of individual animals is known, we suggest that this would be difficult to prove conclusively (see also Both 2007, Jonzén et al. 2007). For migratory animals, detection is further complicated by environmental influences, e.g. temperature, at a range of locations (Gordo et al. 2005, Mitrus et al. 2005, Pulido 2007, this issue).

In Fig. 1, we provide 3 (from a larger potential number) temperature relationships and suggest what they might tell us. The first suggests the same temperature response across time, while the second and third examples provide evidence of change above and beyond that which can be explained by temperature. In phenological studies, it is normally assumed, implicitly or explicitly, that response to temperature remains

\*Email: ths@ceh.ac.uk

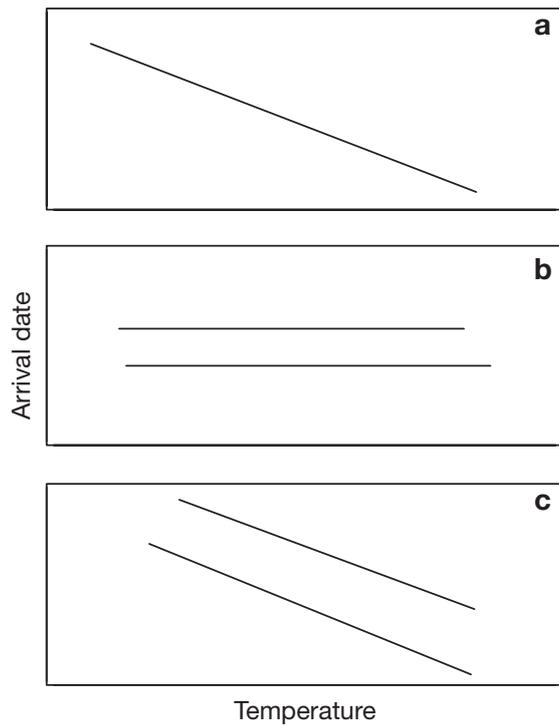


Fig. 1. Three possible relationships between arrival date (vertical axis) and temperature (horizontal axis), where 2 lines are present they represent 2 separate time periods. (a) Phenological plasticity remains constant over time; (b) no phenological plasticity but a step change or gradual drift to earlier arrival; (c) phenological plasticity and earlier arrival for a given temperature than previously (shown here as parallel relationships, but need not be)

constant over time, and can be used to predict future changes. Some of these step or gradual changes could be attributable to a considerable northwards shift in wintering areas, although this is much more likely in short-distance than transcontinental migrants. Indeed, it would be difficult to attribute these additional changes to either individual learning/adaptation or population evolution without knowledge of individual birds. However, in white storks *Ciconia ciconia*, for example, we know that early birds are consistently early, that early birds nest early, and contribute more young to successive generations (Tryjanowski et al. 2004). Therefore, all other things being equal, we might expect trends to earlier arrival to lead to evolutionary change.

In the present paper, we analysed two 56 yr time series on migration phenology of 2 hirundine species in England. The first is of the sand martin *Riparia riparia*, a bird species that was reported as consistently earlier in its first arrival dates in Europe (Lehikoinen et al. 2004). The sand martin

winters in western Africa, north of the equator, and departs for the UK in March (Wernham et al. 2002). We compare changes in its arrival dates with another frequently recorded hirundine, the barn swallow *Hirundo rustica*. The barn swallow winters in southern Africa and departs for the UK in late February/March (Wernham et al. 2002). The migration routes of the 2 species are likely to overlap north of the equator. Historically, in the UK, there has been some evidence for later first arrival dates in the sand martin than in the barn swallow (Table 1; means: April 19 cf. April 13).

In the present paper, we analyse the data for changes over time and responses to temperatures along migration routes, and examine for supra-temperature (i.e. that cannot be explained by temperature) effects that may provide evidence of genetically based adaptation. We believe that by focussing the study on 2 very similar species, we create an opportunity to understand how species may react in different ways to temperature change, as suggested by Pertoldi & Bach (2007).

## 2. MATERIALS AND METHODS

### 2.1. Bird data

Data on the first arrival dates of sand martin *Riparia riparia* and barn swallow *Hirundo rustica* were taken from 8 'bird reports' in England (Table 2). A restriction of observation years to 1950–2005 was made to ensure that records in each year came from at least 4 of the reports. Dates were converted to days post-December 31. To create a single mean value, 2-way ANOVA was undertaken on first dates of each species with Year and Site as factors. The resulting (least-square) means for each year were calculated with 'missing plot' estimates for absent data. In reality, these means were very close to the unadjusted means (sand martin:  $r = 0.999$ , barn swallow:  $r = 0.993$ , both  $p < 0.001$ ).

Table 1. *Riparia riparia* and *Hirundo rustica*. A selection of mean arrival dates from sources in the UK prior to 1950. <sup>a</sup>: taken as the mean of extreme dates

Year range	Recorder	Location	Arrival dates	
			<i>R. riparia</i>	<i>H. rustica</i>
1768–1793	Gilbert White	Hampshire	Apr 1 <sup>a</sup>	Apr 8 <sup>a</sup>
1768–1793	William Marwick	Sussex	Apr 27 <sup>a</sup>	Apr 17 <sup>a</sup>
1818–1830	Revett Sheppard	Essex	Apr 22	Apr 14
1828–1843	Henry Doubleday	Essex	Apr 11	Apr 10
1820–1849	Leonard Jenyns	Cambs	May 7	Apr 21
1865–1884	Thomas Preston	Wiltshire	Apr 17	Apr 5
1887–1907	R. B. Caton	Norfolk	Apr 17	Apr 14

Table 2. *Riparia riparia* and *Hirundo rustica*. Sources of data for the present study, in order of increasing latitude. <sup>a</sup>55 for *R. riparia*

Location	Years	Source	No. of yr of records
Sussex	1960–2005	Sussex Bird Report	45
Bristol	1950–2005	Avon Bird Report	53
Essex	1950–2004	Essex Birds	55
Suffolk	1950–2005	Suffolk Birds	55
Leicestershire	1954–2004	Birds of Leicester and Rutland	50
Sheffield	1973–2004	Birds of the Sheffield Area	32
Barnsley	1970–2005	Barnsley Bird Study Group	36
Wharfedale	1950–2005	Wharfedale Naturalist Society	56 <sup>a</sup>

Neither species is undergoing population decline in the UK ([www.bto.org.uk](http://www.bto.org.uk)), so it is unlikely that population changes have affected the timing of detection of first arrivals (Sparks et al. 2001, Tryjanowski et al. 2005).

## 2.2. Temperature data

We have taken monthly temperatures for the years 1950 to 2005 from the UEA Climatic Research Unit's CRUTEM2v 5° × 5° gridded dataset ([www.cru.uea.ac.uk](http://www.cru.uea.ac.uk)). These data are anomalies from the 1961 to 1990 average for terrestrial environments. Mean temperature anomalies were calculated for each of 5 regions: southern Africa 20 to 35° S, 10 to 35° E (representing the wintering areas of the barn swallow), SW Africa 10° N to 20° S, 10 to 20° E (representing part of the barn swallow migration route), W Africa 5 to 35° N, 20° W to 5° E (representing the likely wintering area of sand martin and migration route of both species), SW Europe 35 to 50° N, 10° W to 0° (representing the migration route of both species within Europe), and England and Wales 50 to 55° N, 5° W to 0° (representing the main destination of both species).

## 2.3. Statistical analysis

Regression and correlation techniques were used to compare mean first arrival date in each year with year (to examine for changes over time) and with temperatures in some or all of the examined geographical regions. Forward stepwise regression was used to select a model of arrival date based on geographic regional temperatures pertinent to each species. The model selected was that in which all coefficients were statistically significant, and the sum of the significant regression coefficients was used to estimate the effect of a 1°C increase in temperature on arrival date. The 56 yr series was divided into 2 halves of 28 yr each (1950 to 1977 and 1978 to 2005) to examine for consistency

of temperature response. Comparison of slopes between the 2 periods or between the 2 species was done using standard regression techniques. All analyses were done with the Minitab statistical package.

## 3. RESULTS

The mean first arrival date of the sand martin *Riparia riparia* (March 24) was significantly earlier over the 56 yr than that of the barn swallow *Hirundo rustica* (March 30; paired  $t_{55} = -7.66$ ,  $p < 0.001$ ). Linear

regression suggests significantly earlier arrival of both species over the study period (sand martin:  $F_{1,54} = 57.34$ ,  $p < 0.001$ ; barn swallow:  $F_{1,54} = 17.04$ ,  $p < 0.001$ ), although the trend ( $\pm$ SE) is much greater for sand martin ( $-0.38 \pm 0.05$ ) than for barn swallow ( $-0.16 \pm 0.04$ ) ( $F_{1,108} = 11.84$ ,  $p = 0.001$ ). The patterns of migration phenology over time are dissimilar (Fig. 2), and this is made clearer when plotting the differences between the 2 series (Fig. 3). Correlations with temperatures (Table 3) reveal 2 key features: that correlations between sand martin and temperature are typically higher than those for barn swallow; and that correlations with temperatures in Europe are generally higher than those in Africa. Temperatures appear to have been rising faster in Europe than in Africa (Table 4).

Fig. 4 shows the tighter relationship of sand martin arrivals to March temperatures in SW Europe, and some hint of a non-linear response to temperature. Fig. 4 also identifies the 2 halves of the time series separately, and it is clear that for sand martin arrivals are now earlier than temperatures would previously have suggested. Stepwise regression for sand martin arrivals suggests that March temperatures in SW Europe ( $b = -3.0$ ,  $p = 0.008$ ), W Africa ( $b = -3.8$ ,  $p =$

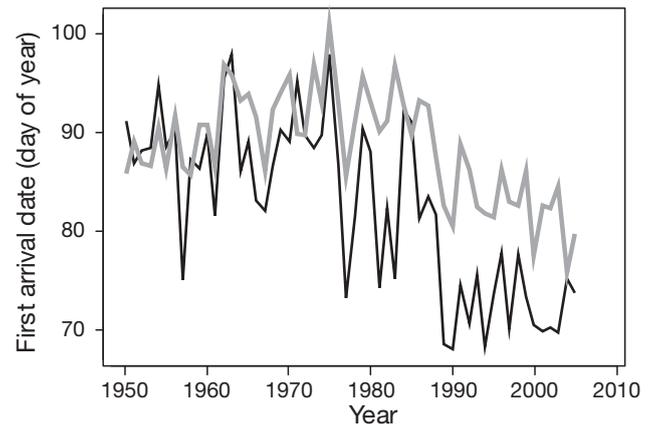


Fig. 2. *Riparia riparia* and *Hirundo rustica*. Mean first arrival dates of *R. riparia* (black) and *H. rustica* (grey)

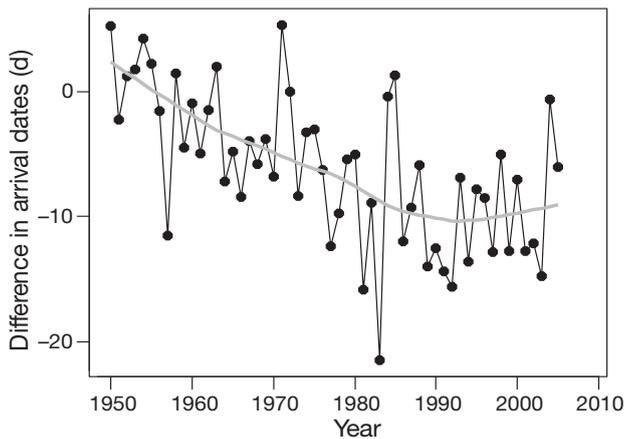


Fig. 3. *Riparia riparia* and *Hirundo rustica*. Difference between *R. riparia* and *H. rustica* arrival dates; negative values implying earlier arrival of *R. riparia* ( $r = -0.59$ ,  $p < 0.001$ ). A distance weighted (lowess) line (grey line) shows the underlying pattern

0.003) and England & Wales ( $b = -1.9$ ,  $p = 0.013$ ) account for 65.4% of the variation in arrival dates ( $F_{3,52} = 32.75$ ,  $p < 0.001$ ). The combined coefficients suggest a  $1^{\circ}\text{C}$  increase across the migration route in March would advance sand martin arrival by 8.7 d. A stepwise regression model for barn swallow accounts for 58.4% of the variation in barn swallow arrival dates ( $F_{4,50} = 17.52$ ,  $p < 0.001$ ) and includes February ( $b = +4.2$ ,  $p = 0.015$ ) and March ( $b = -7.3$ ,  $p < 0.001$ ) temperatures in SW Africa, March temperatures in SW Europe ( $b = -1.6$ ,  $p = 0.003$ ), and February temperatures in England & Wales ( $b = -0.7$ ,  $p = 0.035$ ). The combined coefficients suggest that a  $1^{\circ}\text{C}$  increase in temperature in the selected months and locations would advance barn swallow arrival time by 5.4 d.

Table 3. *Riparia riparia* and *Hirundo rustica*. Correlations of first arrival dates with mean temperature anomalies, values in bold are statistically significant ( $p < 0.05$ )

Region	Month	<i>R. riparia</i>	<i>H. rustica</i>
Southern Africa	Jan		-0.07
	Feb		<b>-0.27</b>
	Mar		-0.19
SW Africa	Jan		-0.22
	Feb		-0.20
	Mar		<b>-0.55</b>
W Africa	Jan	-0.01	-0.04
	Feb	-0.19	-0.15
	Mar	<b>-0.56</b>	<b>-0.45</b>
SW Europe	Jan	-0.18	-0.08
	Feb	<b>-0.37</b>	<b>-0.39</b>
	Mar	<b>-0.75</b>	<b>-0.58</b>
England & Wales	Jan	<b>-0.36</b>	<b>-0.29</b>
	Feb	<b>-0.40</b>	<b>-0.51</b>
	Mar	<b>-0.63</b>	<b>-0.53</b>

Table 4. Regression estimates of changes in monthly temperature anomalies in 5 geographic areas. Regression estimates ( $b$ ) in bold are significant ( $p < 0.05$ )

Region	Parameter	Feb	Mar
Southern Africa	$b$	<b>0.022</b>	<b>0.017</b>
	SE	0.004	0.004
	$p$	<0.001	<0.001
SW Africa	$b$	<b>0.008</b>	<b>0.012</b>
	SE	0.004	0.004
	$p$	0.042	0.003
W Africa	$b$	<b>0.012</b>	<b>0.022</b>
	SE	0.005	0.005
	$p$	0.030	<0.001
SW Europe	$b$	<b>0.022</b>	<b>0.025</b>
	SE	0.011	0.009
	$p$	0.041	0.005
England & Wales	$b$	0.029	<b>0.027</b>
	SE	0.015	0.011
	$p$	0.057	0.019

Extending the model to include separate regression lines for the two 28 yr periods is highly significant for sand martin ( $p < 0.001$ ), suggesting 6.5 d earlier arrival in the recent period than the earlier period at equivalent temperatures. A similar addition to the barn swallow model was not quite significant ( $p = 0.069$ ), but suggested earlier arrival in the recent period by 2.0 d.

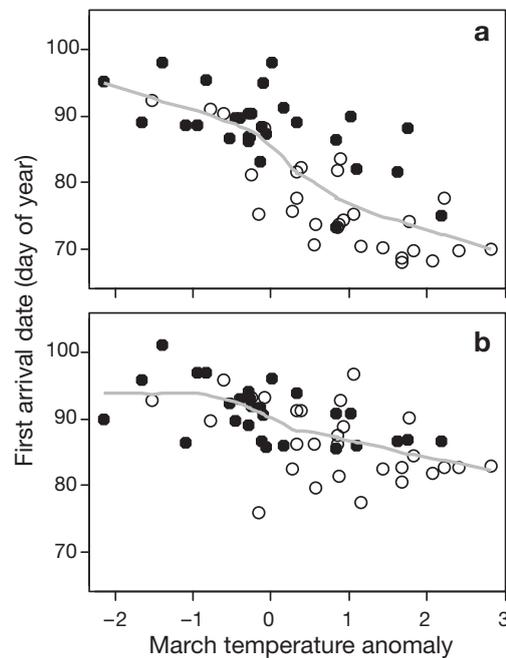


Fig. 4. *Riparia riparia* and *Hirundo rustica*. Relationships between (a) *R. riparia* and (b) *H. rustica* mean first arrival dates and March temperature in SW Europe. A lowess line identifies the underlying pattern. Solid and open symbols represent years in the 1950 to 1977 and 1978 to 2005 periods, respectively

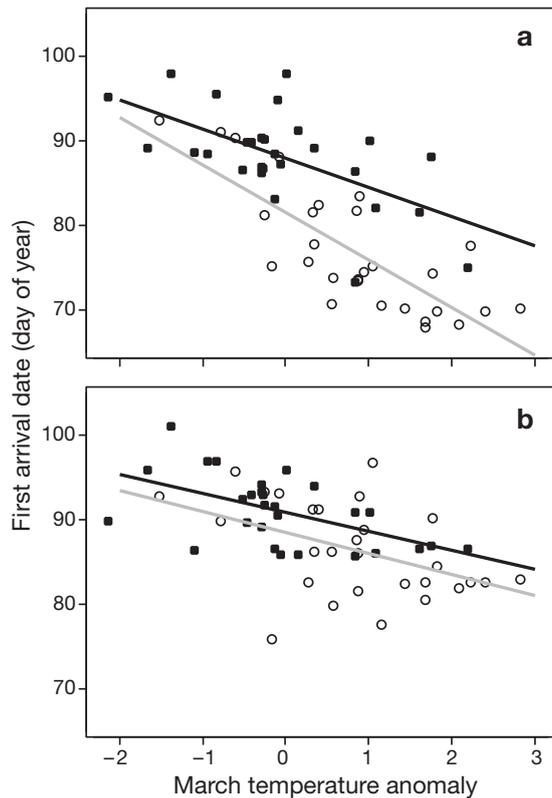


Fig. 5. *Riparia riparia* and *Hirundo rustica*. Relationship between (a) *R. riparia* and (b) *H. rustica* mean first arrival dates and March temperature in SW Europe. Regression lines represent the relationship in the 1950 to 1977 (black line, solid symbols) and 1978 to 2005 (grey line, open symbols) periods

It is difficult to show these changes in multiple dimensions so Fig. 5 depicts only the relationship with temperature in SW Europe where the additional change in sand martin is clear.

#### 4. DISCUSSION

The migration routes of the 2 species are likely to be similar north of the equator; the main difference being the additional sub-equatorial journey undertaken by the barn swallow *Hirundo rustica*. Historically, sand martin *Riparia riparia* arrived in England later than barn swallow, but in recent years the sand martin has become much, and consistently, earlier. For sand martin, there is for recent years a significantly earlier arrival at the same temperatures; the equivalent pattern for barn swallows is smaller and not quite significant. These results clearly point to the fact that these 2 species have changed at different rates to one another, so we should not expect all species to respond to temperature in similar ways. There is strong evidence of change in sand martin that can be attributed

to modified behaviour. Whilst it is likely that this results from evolutionary change, the possibility of adapted behaviour by individual birds, or other causes, cannot be ruled out. The difficulties in detecting evolutionary change are discussed in detail by Pulido (2007).

The data used here were derived from amateur recording schemes, which were not carried out under strict recording protocols (cf. Tryjanowski et al. 2005). There is a possibility that the detection of first birds has been affected by increasing recorder effort. However, we do not feel that this is an issue with the 2 species considered here, because they are highly visible and numerous, and their habitats are frequently monitored. Moreover, the changes reported here, and the greater change in sand martin, are also reported from schemes with constant recording effort (e.g. Sparks et al. 2006). In addition, we have averaged across 8 different reports to further reduce sources of error.

Migration timing can be modified by evolutionary processes, because arrival time affects the time of breeding (Turner 1982, 2006, Tryjanowski et al. 2004, Newton 2007, Rubolini et al. 2007). The link between spring migration and breeding is probably due to changes in food sources. In Scotland, for example, aphids have occurred earlier during recent decades (Sparks et al. 2006), and are an important food source for both species, but especially for sand martin (Turner 2006). Ambient temperature can also affect the condition of birds via an effect on food availability and/or the costs of thermoregulation (Pertoldi & Bach 2007).

Is the trend strongest for sand martin because it is smaller (14 vs. 20 g for barn swallows) and smaller birds react faster to temperature (Stevenson & Bryant 2000, Bradshaw & Holzapfel 2006)? Moreover, sand martins forage on smaller insects than barn swallows, both at wintering as well as at breeding grounds (Turner 1982, 2006, Koppj 2000), and the abundance of smaller insects is known to be more closely related to weather, especially positively to temperature (Bradshaw & Holzapfel 2006). The factors determining when barn swallows and sand martins commence spring migration are unknown, but changes in daylength, in weather, and in the food supply, both at wintering grounds and on the migration route, are likely to be important (Berthold 2001, Newton 2006, Turner 2006).

Migration phenology may also be influenced by other factors not considered here, and the use of finer scale temperatures or other variables may be appropriate. Most likely, migration is faster because environmental conditions during migration have improved (Huin & Sparks 1998, Gordo et al. 2005, Rubolini et al. 2007). However, it appears clear that sand martins are arriving now considerably earlier than barn swallows, seem more temperature responsive, and appear to have had a greater supra-temperature change.

1978 to 2005 was a period of rapid climate warming, and the migratory behaviour of birds was different compared to the more stable period from 1950 to 1977. The displacement of the 2 regression lines in Fig. 5 suggests that the changes cannot merely be attributed to (linear or non-linear) phenotypic plasticity, because arrival in 1978 to 2005 was earlier than in 1950 to 1977 at the same temperature, particularly for sand martin.

We suggest that both phenotypic plasticity and microevolutionary changes have occurred, and that they are not necessarily mutually exclusive (Gienapp et al. 2007, this issue, but cf. Jonzén et al. 2007). We do not provide genetic evidence that is crucial to prove microevolutionary response to climate change (Møller & Merilä 2004, Bradshaw & Holzapfel 2006). However, arrival date, at least in the barn swallow, is heritable (Møller 2001), which supports the microevolutionary point of view. Migratory changes may be quite rapid in birds, and, under intense artificial selection in captive birds, some types of genetically controlled change have occurred in only 3 to 6 generations (cf. Pulido & Berthold 2004). Recently, there may have been a strong selection for earlier and faster migration and, in consequence, earlier arrival in the 2 species considered here.

In conclusion, we show that both analysed hirundine species responded to changed temperature, and, in particular, the marked changes in sand martin support the possibility of adaptation in recent decades.

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