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Proc. R. Soc. B published online 9 November 2011
doi: 10.1098/rspb.2011.1897

References

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Published online 9 November 2011 in advance of the print journal.

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Novel methods reveal shifts in migration phenology of barn swallows in South Africa

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Many migratory bird species, including the barn swallow (*Hirundo rustica*), have advanced their arrival date at Northern Hemisphere breeding grounds, showing a clear biotic response to recent climate change. Earlier arrival helps maintain their synchrony with earlier springs, but little is known about the associated changes in phenology at their non-breeding grounds. Here, we examine the phenology of barn swallows in South Africa, where a large proportion of the northern European breeding population spends its non-breeding season. Using novel analytical methods based on bird atlas data, we show that swallows first arrive in the northern parts of the country and gradually appear further south. On their north-bound journey, they leave South Africa rapidly, resulting in mean stopover durations of 140 days in the south and 180 days in the north. We found that swallows are now leaving northern parts of South Africa 8 days earlier than they did 20 years ago, and so shortened their stay in areas where they previously stayed the longest. By contrast, they did not shorten their stopover in other parts of South Africa, leading to a more synchronized departure across the country. Departure was related to environmental variability, measured through the Southern Oscillation Index. Our results suggest that these birds gain their extended breeding season in Europe partly by leaving South Africa earlier, and thus add to scarce evidence for phenology shifts in the Southern Hemisphere.

Keywords: climate change; bird migration; life cycle timing; phenology shift; Southern Oscillation Index

1. INTRODUCTION

Migratory birds are now arriving in Europe earlier than they used to 20 years ago [1,2]. They are thought to respond to warmer springs and the earlier onset of optimal breeding conditions compared with the late twentieth century. However, not all populations arrive early enough to keep step with the changing conditions, and this has led to declines in populations that are not reacting fast enough [3,4]. The migratory journey imposes a constraint on the ability of long-distance migrants to react to changing conditions in their European breeding grounds [5,6]. It remains unclear whether the observed advancement in north-bound pre-breeding migration [7,8] is due to improved conditions en route allowing faster migration, earlier departure from the non-breeding grounds or birds wintering closer to their breeding grounds [9]. Further, little is known about the cues that long-distance migrants use to start their return journey towards the breeding grounds. Whether they use fixed cues like day length and endogenous migration programmes [5] or whether departure time depends on environmental variation [10] affects their ability to respond to climate change at their breeding grounds. For example, birds could use correlations between large-scale weather patterns to predict conditions at the breeding grounds [11]. Phenological studies of long-distance migrants at their non-breeding grounds are

urgently needed to address these questions, which have been identified as priority research areas in the study of bird migration and climate change [2].

When studying phenological shifts, two kinds of data have been predominantly used. The most widely available data are observations of first arrival dates (i.e. the first time an individual of a species is observed in a given season in a particular area). This kind of data is strongly influenced by the probability of detecting such individuals, which can be subject to trends in bird population sizes [12] and observer awareness or effort. The second type of data commonly used is count or ringing data from localized bird observatories. These data allow examination of mean migration dates and other aspects of migratory phenology, but are restricted to specific localities and thus potentially vulnerable to shifts in geographical migration patterns or local weather conditions. Unfortunately, datasets analysed to date almost always suffer from one of these two drawbacks [1]. In contrast to the phenology of arrival in the breeding ground and egg laying, much less is known about the timing of other important phenological events such as moult and departure from the breeding grounds (but see [13]). A critical gap in our knowledge is the timing of arrival and departure of migrants to and from their non-breeding grounds [14].

Here, we examine possible changes in phenology of barn swallows (*Hirundo rustica*) in their South African non-breeding grounds. We use a novel approach of analysing bird atlas data from the Southern African Bird

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Atlas Projects (<http://sabap2.adu.org.za/>), which are collected over large spatial areas and throughout the year over multiple years. Using nonlinear regression models, we quantify the arrival and departure patterns of barn swallows in three distinct regions of South Africa (from north to south): Gauteng, KwaZulu-Natal and Western Cape. For each region, the arrival and departure times from the first atlas, covering the years 1987–1991, are compared with the arrival and departure times from the second atlas, covering the years 2007–2011.

2. METHODS

(a) Data collection

We used data collected under the two Southern African Bird Atlas Projects (SABAP1: 1987–1991; and SABAP2: 2007 to present—we included data up until January 2011). These data were collected as checklists by registered volunteer atlasers. Atlasers recorded all bird species they saw within a period of up to 5 days in a particular grid cell (excluding those SABAP1 lists that were collected over longer time intervals). For SABAP1, the cells were quarter-degrees, whereas they were $5 \times 5'$ for SABAP2.

Barn swallows arrive in the far south of South Africa later than in the north of the country. We therefore analysed three regions of the country separately: Gauteng (13 897 checklists), KwaZulu-Natal (4406 checklists) and Western Cape (7667 checklists; note that the study regions do not match the political boundaries, but we use these names for convenience). Each region has a relatively homogeneous probability of barn swallows being observed, and a substantial dataset. The rectangle delimited by the left upper corner $25^\circ\text{S } 27^\circ\text{E}$ and the right lower corner $27^\circ\text{S } 29^\circ\text{E}$ is the Gauteng province and surroundings. The KwaZulu-Natal block is delimited by the left upper corner $29^\circ\text{S } 29^\circ\text{E}$ and the right lower corner $30^\circ\text{S } 31^\circ\text{E}$, and Western Cape is the block with the left upper corner $32^\circ30'\text{S } 17^\circ\text{E}$ and the right lower corner $35^\circ\text{S } 20^\circ\text{E}$.

We grouped all checklists by 5-day interval (pentade) into which their starting date fell, using the fixed-date system proposed by Berthold [15] and commonly used in bird migration research. Our data unit for the analysis is the proportion of checklists in each pentade recording barn swallows (reporting rate R), weighted by the total number of checklists collected during that pentade. Barn swallows arrive in South Africa around September, spend the Southern Hemisphere summer here, and start their northward migration again in April. For the analysis, we split the year in mid-winter (between pentades 37 and 38; i.e. we take the phenological year as from 5 July of one year to 4 July of the next), when barn swallows are virtually absent. We define the Southern Hemisphere pentade P_{SH} in relation to Berthold's pentade P_B as $P_{\text{SH}} = P_B + 36$ if $P_B < 37$, and $P_{\text{SH}} = P_B - 37$ otherwise.

(b) Statistical analyses

We used a nonlinear curve fitting algorithm implemented in procedure `nls` (nonlinear least squares) in program R v. 2.12.0 [16] to fit the following curve to our data. We supplied the number of checklists to `nls` using the ‘weights’ statement, which causes `nls` to use weighted least squares as the objective function. The weights should be the inverse of the variance for each observation, which we took to be inversely proportional to the number of checklists. The fitted

curve consists of two sigmoid curves (logistic functions) pasted back to back so that their asymptotes are the same:

$$R = \begin{cases} \frac{Asym}{1+\exp[-(P_{\text{SH}}-xmid_a)/scal_a]} + \varepsilon, & \text{if } P_{\text{SH}} \leq 43 \\ \frac{Asym}{1+\exp[-(P_{\text{SH}}-xmid_d)/scal_d]} + \varepsilon, & \text{if } P_{\text{SH}} > 43, \end{cases} \quad (2.1)$$

where R is the reporting rate (i.e. the proportion of checklists reporting barn swallows), and P_{SH} the Southern Hemisphere pentade. The five structural parameters to be estimated are as follows. $Asym$ is the maximum average reporting rate reached in mid-summer when barn swallows are most abundant ($P_{\text{SH}} = 43$ ends 30 January), $xmid_a$ and $xmid_d$ are the inflection points (i.e. half of the maximum) of the sigmoid curves relating to arrival and departure periods, respectively, and $scal_a$ and $scal_d$ are the scale parameters, which can be interpreted as rate of arrival or departure, respectively. Note that the curves share the same asymptote. Finally, we assumed normally distributed errors, ε , and verified the validity of this assumption by inspecting the residual plots.

The effect of atlas period and other covariates on phenology can be examined by making the parameters (e.g. the $xmid_a$) functions of these covariates (x_i), with coefficients β to be estimated:

$$xmid_a = \beta_0 + \sum \beta_i x_i.$$

First, we examined differences between the two atlas periods without including any environmental covariates. For this, we considered eight variants of the basic model (table 1). Model 1 allowed all five parameters of equation (2.1) to differ between the two atlas periods. Model 8 assumed all parameters to be equal between periods. The other models represent all possible combinations of variable arrival (described by the two parameters $xmid_a$ and $scal_a$), departure (described by $xmid_d$ and $scal_d$), and asymptote ($Asym$) across periods. We then used Akaike’s information criterion (AIC) to rank these models [17]. We fitted the same eight models to each of the three regions separately.

Next, we examined possible causes of variation in phenology by making arrival ($xmid_a$), asymptote ($Asym$) and departure ($xmid_d$) functions of environmental covariates. We chose annual average values for the Southern Oscillation Index (SOI), defining the years to go from June to May to maximize the coherence of individual Southern Oscillation events [18]. SOI positively correlates with summer (November to April) precipitation in Southern Africa and negatively with precipitation in the eastern equatorial regions of Africa [18] where barn swallows pass through on their migration journey. If large-scale weather patterns affect the timing and extent to which barn swallows migrate into this region, we expect SOI to correlate with annual arrival and departure dates, and the maximum reporting rate, which is linked to abundance [19]. We downloaded the SOI data from <http://www.cgd.ucar.edu/cas/catalog/climind/> on 25 August 2011.

3. RESULTS

For Gauteng, the AIC best model (model 3, table 1) showed that barn swallows departed South Africa on average 8 days earlier (1.53 pentades, s.e. = 0.30; see table 2 for all parameter estimates) during the 2007–2011 atlas than during the 1987–1991 atlas (figure 1). Also, the maximum proportion of checklists recording barn swallows was approximately 5 per cent lower in 2007–2011 when compared with 1987–1991.

Table 1. Model selection analysis of barn swallow migration phenology in South Africa. The model column indicates which part(s) of the model were allowed to vary between the two atlases (1987–1991 versus 2007–2011). ‘Asym’ refers to the asymptote (i.e. the maximum reporting rates). ‘Arrival’ is the timing of arrival in the Southern Hemisphere spring, whereas ‘departure’ refers to the timing of departure in autumn. Arrival and departure are determined by two parameters each, the location of the midpoint and scale of the respective part of the sigmoid curve. K is the total number of parameters estimated for each model (including one parameter for the residual variance). We evaluated the models using Akaike’s information criterion (AIC). ΔAIC gives the difference in AIC between the current model and the best (in italics), and w is Akaike weight, showing the relative support each model has compared with the others. See table 2 for model-averaged parameter estimates.

model	K	Gauteng		KwaZulu-Natal		Western Cape		
		ΔAIC	w	ΔAIC	w	ΔAIC	w	
1	Asym, arrival, departure	11	2.09	0.26	5.17	0.03	4.88	0.05
2	Asym, arrival	9	20.99	0	2.16	0.13	5.41	0.04
3	Asym, departure	9	0	0.73	2.81	0.09	2.01	0.21
4	Asym	7	17.92	0	0	0.37	6.18	0.03
5	arrival, departure	10	8.48	0.01	3.16	0.08	3.53	0.10
6	arrival	8	32.87	0	0.65	0.27	10.12	0
7	departure	8	10.96	0	7.73	0.01	0	0.56
8	none	6	34.22	0	5.14	0.03	6.60	0.02

Table 2. Parameter estimates for nonlinear regression models fitted to Southern African Projects Bird Atlas barn swallow records. The estimates (Est) in 5-day intervals (pentades) are averaged across all models (shown in table 1), using Akaike weights. The confidence intervals (LCL, lower confidence limit; UCL, upper confidence limit) are based on unconditional standard errors, which account for model selection uncertainty (methods followed the study of Burnham & Anderson [17]). The models consist of two sigmoid curves, as described in equation (2.1). In addition, we estimated the difference between the two atlases in all parameters (Δ); negative values mean a lower estimate for SABAP2 (2007–2011) when compared with SABAP1 (1987–1991).

	Gauteng			KwaZulu-Natal			Western Cape		
	Est	LCL	UCL	Est	LCL	UCL	Est	LCL	UCL
asymptote	0.76	0.75	0.77	0.78	0.74	0.82	0.68	0.65	0.72
Δ asymptote	-0.05	-0.07	-0.02	0.06	-0.03	0.16	0.01	-0.02	0.04
midpoint of arrival	20.77	20.50	21.04	24.83	23.70	25.96	27.46	26.68	28.25
Δ midpoint of arrival	0.09	-0.24	0.42	-1.10	-3.73	1.54	0.18	-0.51	0.87
scale of arrival	1.60	1.37	1.84	3.67	2.82	4.52	4.18	3.59	4.78
Δ scale of arrival	0.03	-0.15	0.20	-0.66	-2.43	1.10	0.10	-0.35	0.56
midpoint of departure	57.26	56.99	57.53	56.86	56.41	57.31	55.44	54.93	55.94
Δ midpoint of departure	-1.53	-2.08	-0.98	-0.08	-0.46	0.30	1.08	0.07	2.10
scale of departure	-1.22	-1.44	-0.99	-1.38	-1.77	-0.99	-1.82	-2.25	-1.40
Δ scale of departure	0.05	-0.40	0.51	0.05	-0.24	0.33	0.53	-0.29	1.35

There is evidence that barn swallows also follow different temporal migration patterns now when compared with 20 years ago in both of the other studied regions of South Africa. In KwaZulu-Natal, the top three models had a combined weight of 0.77, and the model-specific parameter estimates suggest that swallows are arriving 14 days earlier (2.90 pentades, s.e. = 0.82) or that the maximum reporting rate was approximately 10 per cent (s.e. = 2.3) higher in 2007–2011. For the Western Cape region, the models suggest a later departure by 6 days (1.23 pentades, s.e. = 0.43), but with little or no change in average arrival date or maximum reporting rate. Table 2 gives model-averaged parameter estimates.

Across the three study regions, barn swallows departed over a shorter time interval during 2007–2011 than they did 20 years earlier. During 1987–1991, the mean departures dates fell into the 1–5 April pentade (midpoint of fitted logistic model = 54.8, s.e. = 0.4) in the Western Cape, where the swallows left first, and into the 16–20

April pentade (58, s.e. = 0.2) in Gauteng, where they left last. Together with their sharp departures, this 15-day spread meant dramatic differences between regions. Twenty years later, these departures were more synchronous, and in all three regions mean departure is now during the 11–15 April pentade.

Our analysis shows previously undocumented variation in the residence times of barn swallows across South Africa. The birds spent on average 182 days in Gauteng (time span between the midpoints of arrival and departure; table 2), 160 in KwaZulu-Natal and only 140 days in the Western Cape. In all three regions, arrival was more gradual than departure (figure 1; the absolute value of the scale parameter was larger for arrival than departure, table 2). This pattern was most pronounced in the southernmost region we studied—the Western Cape. None of the scale parameters significantly differed between the two atlas periods (table 2), suggesting that the spread in arrival and departure remained broadly unchanged.

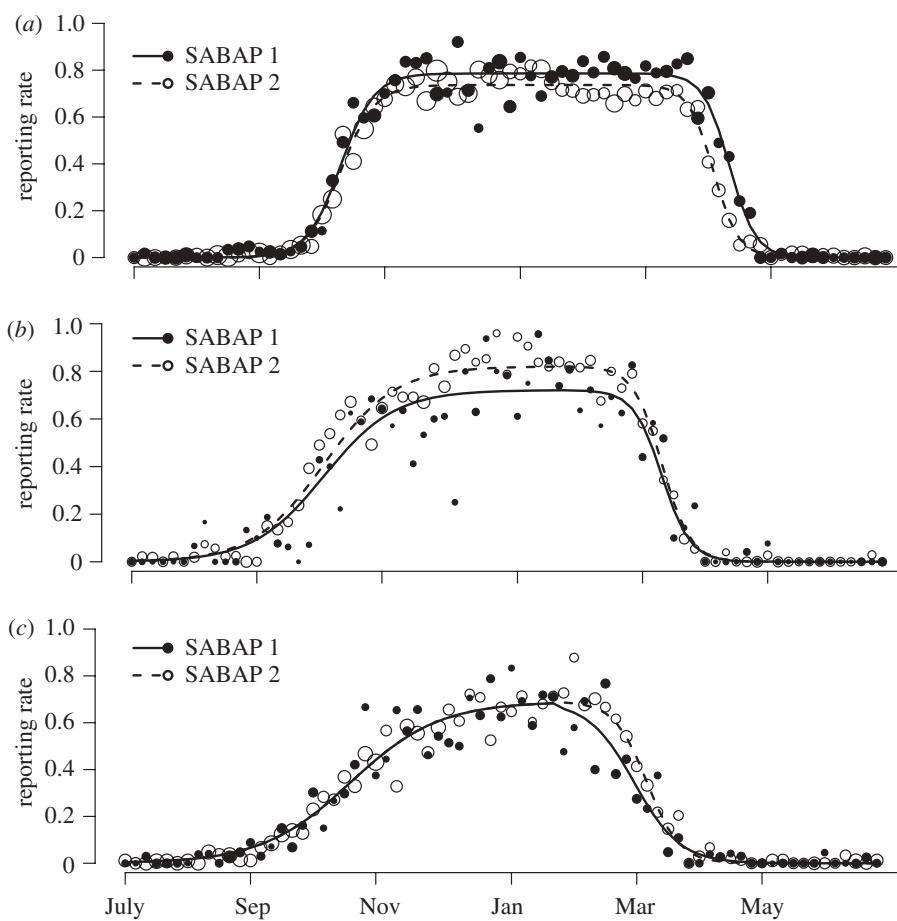


Figure 1. The proportion of checklists recording barn swallows throughout the year in three different areas of South Africa during 1987–1991 (SABAP1, solid lines with filled circles) and 2007–2011 (SABAP2, dashed lines with open circles): (a) Gauteng, (b) KwaZulu-Natal and (c) Western Cape. The circles show the observed proportions per 5-day interval and the lines are the best-fitting curves produced by the model with the lowest AIC value (table 1). The area of the symbols is proportional to the number of checklists, with the circles depicted in the legend representing 40 lists (same scale in all three panels).

To examine possible environmental effects on barn swallow migration phenology, we related arrival, maximum reporting rate and departure to the SOI for all three regions. Departure of barn swallows from Gauteng was negatively related to SOI (-0.31 , s.e. = 0.11, $t = -2.85$, $p < 0.005$), and we found a similar effect, albeit not significant, for the Western Cape (-0.27 , s.e. = 0.15, $t = -1.79$, $p = 0.07$). All other parameters were not significantly related to SOI ($p > 0.15$).

4. DISCUSSION

Our analysis suggests a shift in phenology of barn swallow migration in South Africa between the two atlas periods. Yet the pattern varied spatially within South Africa. In the northernmost province, Gauteng, barn swallows left 8 days earlier during 2007–2011 than in 1987–1991. They did not change their departure from the KwaZulu-Natal region over the same time period, but in the Western Cape, the southernmost region, departures are now 6 days later. In contrast, we found no evidence for a change in the arrival date at any of the three South African non-breeding grounds studied, although there was a tendency for earlier arrival in KwaZulu-Natal.

Barn swallows have advanced their arrival date at their European breeding grounds [4,20,21] and either advanced [21] or delayed their departure after the

breeding season [13,22]. A prolonged breeding season in parts of Europe appears to allow some barn swallows to raise an additional brood [13]. Even though based on two discrete time periods rather than a continuous time series, our results show that barn swallows may achieve their extended breeding season partly by spending less time in their non-breeding grounds. Gauteng is the northernmost South African province we examined and the one for which we had the most data. In this region, barn swallows advanced their departure by a similar amount to their earlier arrival in Europe (4–8 days) [4,20].

In contrast, barn swallows did not shorten their stay in the more southerly regions we examined (the Western Cape and KwaZulu-Natal), where their residence time was shortest. Barn swallows moult in their non-breeding grounds, and full moult of all primary flight feathers takes at least 135 days [23], which is close to the 140 days residence time of barn swallows in the Western Cape. The need to complete moult before undertaking the pre-breeding migration could therefore constrain the ability of these birds to further advance their departure from their most southerly non-breeding areas [24].

Little is known about the environmental cues that influence departure from the non-breeding grounds [2]. Here, we found that departure of barn swallows from parts of South Africa was earlier in years with a high SOI. High SOI indicates high precipitation across large

parts of southern Africa [18], which may mean better conditions for refuelling and moult of barn swallows.

Barn swallows from across Europe mix at their non-breeding grounds in South Africa [25], even though there are indications that birds from Britain and Ireland tend to come to western South Africa, whereas the east of the country hosts proportionally more birds from northern and eastern Europe [26]. The mixed origin of barn swallows in South Africa, and the fact that the trends in post-breeding departure dates from Europe appear to be inconsistent among regions [13,21], may explain the lack of a clear change in arrival dates at the South African non-breeding grounds.

We found that in Gauteng barn swallows are now encountered 5 per cent less often than 20 years ago, which could be either a reflection of their general decline across Europe [27] or an indication that they tend to spend their non-breeding season further north in Africa [9]. However, we found the opposite pattern in KwaZulu-Natal, where barn swallows are now encountered more frequently, and in the Western Cape there was no change in maximum reporting rates between the two atlases.

Our study adds to the evidence of shifting bird phenology in two novel ways. First, it adds to the still-scarce evidence that patterns in the Southern Hemisphere can shed light on changes observed in the Northern Hemisphere [28], as well as adding to the scarce information on phenology of migratory birds in their non-breeding grounds [14]. Second, it uses a novel method that examines phenology throughout the year and across large spatial scales, extending earlier ideas of using atlas data to study bird movement [29,30]. Our data allowed us to examine the change in phenology between two 4-year periods for which atlas data were collected. However, once continuous data are available over a sufficient time period, our method will be able to detect trends in phenology over time, and its dependence on environmental covariates.

We thank the large number of volunteers who collected the bird atlas data, the South African National Biodiversity Institute and other donors of SABAP2 (<http://sabap2.adu.org.za/>) for funding. The analysis and manuscript preparation were supported by grants from the Danish Government, the World University Network and the South African National Research Foundation. We thank Nicola Saino and Piotr Tryjanowski for helpful comments.

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