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Patterns of bird migration phenology in South Africa suggest northern hemisphere climate as the most consistent driver of change

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Abstract

Current knowledge of phenological shifts in Palearctic bird migration is largely based on data collected on migrants at their breeding grounds; little is known about the phenology of these birds at their nonbreeding grounds, and even less about that of intra-African migrants. Because climate change patterns are not uniform across the globe, we can expect regional disparities in bird phenological responses. It is also likely that they vary across species, as species show differences in the strength of affinities they have with particular habitats and environments. Here, we examine the arrival and departure of nine Palearctic and seven intra-African migratory species in the central Highveld of South Africa, where the former spend their nonbreeding season and the latter their breeding season. Using novel analytical methods based on bird atlas data, we show phenological shifts in migration of five species – red-backed shrike, spotted flycatcher, common sandpiper, white-winged tern (Palearctic migrants), and diederik cuckoo (intra-African migrant) – between two atlas periods: 1987–1991 and 2007–2012. During this time period, Palearctic migrants advanced their departure from their South African nonbreeding grounds. This trend was mainly driven by waterbirds. No consistent changes were observed for intra-African migrants. Our results suggest that the most consistent drivers of migration phenological shifts act in the northern hemisphere, probably at the breeding grounds.

Keywords: bird migration, climate change, intra-African migrants, life cycle timing, Palearctic migrants, phenological shift, South Africa, southern hemisphere, waterbirds

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Introduction

Seasonal migratory movement is a fascinating phenomenon of how animals adapt to predictable fluctuations in the environment. Timing of migration events has therefore been an important indicator of how ecosystems react to changes in seasonality, for example due to climate change (Ball, 1990; Root *et al.*, 2003; Parmesan, 2006; Gordo, 2007). Although there is mounting evidence showing shifts in migration phenology of Palearctic bird species at their breeding grounds (Marra *et al.*, 2005; Both & Te Marvelde, 2007; Rubolini *et al.*, 2007; Knudsen *et al.*, 2011), little is known about the phenological shifts at their nonbreeding grounds (Altwegg *et al.*, 2012) and how phenology may react to environmental changes in the southern hemisphere (Chambers *et al.*, 2013). Because climate change patterns are not uniform across the globe (Giorgi, 2006; Garcia *et al.*, 2014), we can expect regional disparities in bird phenological responses. We can also expect these responses to vary across species that show differences in the strength of affinities they have with particular habitats and environments, a factor used to classify species as specialists or generalists.

Among the most widely used data for studying phenological shifts are observations of first arrival dates of migratory birds (i.e. the first time an individual of a species is observed in a given season in a particular area). Patterns in these data are strongly influenced by the detection probability of the studied bird species, which depends on bird population size (Tryjanowski & Sparks, 2001), habitat visibility, species conspicuousness, observer knowledge, and effort (Harrison *et al.*, 1997a). Data from localized bird observatories allow examination of more robust metrics of migration phenology such as mean migration dates. However, these data are restricted to specific localities and thus potentially affected by shifts in geographical migration patterns or local weather conditions. Data sets analysed to date almost always suffer from one of these two drawbacks (Rubolini *et al.*, 2007). However, novel analytical

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methods enable us to examine phenology throughout the year and across large-spatial scales using bird atlas data (Altwegg *et al.*, 2012).

Here, we examine possible changes in phenology of 16 migratory bird species that we considered to be good representatives of the three following groups: Palearctic terrestrial migrants (five species), Palearctic migratory waterbirds (four species), and intra-African migrants (seven species, Table 1), because of their abundance and the robustness of the atlas data. Using nonlinear regression models and bird atlas data from the Southern African Bird Atlas Projects (http://sabap2.adu.org.za/), we quantify the arrival and departure patterns of these migrants in the central Highveld area of South Africa for the periods 1987–1991 and 2007–2012.

The higher latitudes with their strong seasonality have experienced clear shifts towards earlier springs and extended conditions favourable for breeding in birds (Both & Te Marvelde, 2007). We therefore expect Palearctic migrants to shorten their stay at their nonbreeding grounds in South Africa by leaving earlier and possibly arriving later. How climate change affected seasonality in African areas is less clear (Paeth *et al.*, 2009; IPCC, 2013). We would expect inconsistent patterns across the intra-African migrants if they reacted to local changes at their nonbreeding grounds and consistent patterns if migration phenology is driven by conditions at their South African breeding grounds. Finally, we would expect consistent patterns across all species if environmental conditions in South Africa had a strong effect on phenology.

Material and methods

Data collection

We used data collected by the two Southern African Bird Atlas Projects (SAPAB1: 1987–1991, and SABAP2: 2007 and ongoing; for this analysis we included data submitted until January 2012). These data were collected as checklists by registered volunteer atlasers. Atlasers recorded all bird species they identified within a period of up to 5 days in a particular grid cell (those SABAP1 lists which had been collected over longer time intervals were excluded). For SABAP1, the cells were $15' \times 15'$, whereas they were $5' \times 5'$ for SABAP2, so that each 'quarter degree grid cell' for SABAP1 has nine 'pentads' for SABAP2. More information about the SABAP protocols can be found at http://sabap2.adu.org.za/.

Individuals of a migratory bird species generally do not arrive all across South Africa simultaneously (Harrison *et al.*, 1997a; Altwegg *et al.*, 2012). We therefore selected a large enough area to obtain a substantial dataset but in which the migration patterns and the detection probabilities for each species were homogeneous. We selected the rectangle delimited by 23.5°S 26°E at its northwest corner and 27°S 32°E at its southeast corner. This includes the intensely surveyed Gauteng Province and surroundings, and falls at the centre of the region known as the Highveld in South Africa. 3826 and 25044 checklists were collected in this area during SABAP1 and SABAP2, respectively. We grouped all checklists by the 5-day interval into which their starting date fell, using the fixed-date pentade system proposed by Berthold (1973) and commonly used in bird migration research. The year is divided into 73 pentades. For each species s, our data unit for the analysis is the reporting rate R_s, which is calculated for every pentade of the year. R_s is defined as the proportion of checklists in each pentade recording the species s divided by the total number of checklists collected during that pentade. For the analysis, it is convenient to define the start of the phenological year during a time when migrants are absent. In our case, this is during the southern hemisphere mid-winter; whereas Berthold's original system follows the calendar year. We therefore define the southern hemisphere pentade P_{SH} in relation to Berthold's pentade P_B as $P_{\mathrm{SH}} = P_B + 36$ if $P_B < 37$, and $P_{\mathrm{SH}} = P_B - 37$ otherwise.

Statistical analyses

We analysed phenological shifts for each species separately, using the bird atlas data and statistical methods suggested by Altwegg *et al.* (2012). We used a nonlinear curve fitting algorithm implemented in procedure nls (nonlinear least squares) in program R 3.0.1 (R Core Team, 2013) to fit the following curve to our data (Figs 1–3). The fitted curve consists of two sigmoid curves (logistic functions) pasted back to back so that their horizontal asymptotes are the same:

$$R_s = \begin{cases} \frac{\mathrm{Asym}_s}{1+\exp[-(P_{\mathrm{SH}}-\mathrm{xmid}_{a_s})/\mathrm{scal}_{a_s}]} + \varepsilon, & \text{if } P_{\mathrm{SH}} \leq [P_{\mathrm{SH}}]_s \\ \frac{\mathrm{Asym}_s}{1+\exp[-(P_{\mathrm{SH}}-\mathrm{xmid}_{d_s})/\mathrm{scal}_{d_s}]} + \varepsilon, & \text{if } P_{\mathrm{SH}} > [P_{\mathrm{SH}}]_s, \end{cases} \tag{1}$$

where R_s is the reporting rate for species s (i.e. the proportion of checklists reporting species s in a given pentade), and P_{SH} the southern hemisphere pentade. The five structural parameters to be estimated are, for each species, as follows. Asym_s is the maximum average reporting rate of species s reached in mid-summer when the species s is most abundant ($P_{\mathrm{SH}} = [P_{\mathrm{SH}}]_s$, Table 1); xmid_{a_s} and xmid_{d_s} are the inflection points (i.e. half of the maximum) of the sigmoid curves relating to arrival and departure periods of species s; scal_{a_s} and scal_{d_s} are the scale parameters, which can be interpreted as rate of arrival or departure of species s, respectively. Finally, we assumed normally distributed errors, ε, and verified the validity of this assumption by inspecting the residual plots.

Our model essentially divides the phenological year into a part during which migrants arrive ($P_{\mathrm{SH}} \leq [P_{\mathrm{SH}}]_s$) and one during which they depart ($P_{\mathrm{SH}} > [P_{\mathrm{SH}}]_s$). The model assumes that reporting rates are close to zero at the beginning of the phenological year and then monotonically increase when migrants start arriving until they reach a plateau, which for most species happened well before $[P_{\mathrm{SH}}]_s$. Some time after $[P_{\mathrm{SH}}]_s$, we assume that reporting rates decline monotonically to zero as

Table 1 We examine possible shifts in migration phenology of 16 bird species, grouped into three categories, depending on their migration route and ecology. (a) Palearctic terrestrial migrants, (b) Palearctic migratory waterbirds, (c) intra-African migrants

	Common name	Provenance	Breeding	Nonbreeding	$[P_{\mathrm{SH}}]_s$
(a)	European bee-eater *Merops apiaster*	Throughout Eurasian range	Southern Europe and northern Africa to south-western Asia[1a]	Western Africa, south-central Africa and south to ca 27°S in South Africa[1b]	38 (2–6 January)
	Red-backed shrike *Lanius collurio*	Throughout breeding range	Europe, western Asia, north to central Scandinavia, and south to Israel[2a]	Dry savannas of south-eastern Africa, from Kenya southwards, majority in southern Africa[2b]	38 (2–6 January)
	Spotted flycatcher *Muscicapa striata*	Five subspecies occur, widespread provenance	From north-western Africa to most of Europe, to much of central Asia between 36–62°N, east to 117°E[3a]	Sub-Saharan Africa[3b]	51 (8–12 March)
	Steppe buzzard *Buteo buteo*	Eurasia between Finland and Black Sea eastwards	Eastern Europe and Siberia east to 96°E[4a]	Southern Europe, sub-Saharan Africa, and south-western Asia[4b]	44 (1–5 February)
	Willow warbler *Phylloscopus trochilus*	Entire range; the three subspecies occur	From Ireland east and north through Europe to Russian Federation and Ukraine[5a]	Sub-Saharan Africa, south to South Africa[5b]	38 (2–6 January)
(b)	Common sandpiper *Tringa stagnatilis*	Scandinavia and European Russia	30°N to 56°N from western Europe to Japan[6a]	Sub-Saharan Africa east to Australia[6b]	34 (13–17 December)
	Ruff *Philomachus pugnax*	Mostly Asia	From the Netherlands across the northern half of Europe, narrowing across the Arctic and forest tundra zone of Siberia to Chukotskiy[7a]	India, southern Arabia and sub-Saharan Africa (western, central, eastern, and southern)[7b]	24 (24–28 October)
	White-winged tern *Chlidonias leucopterus*	Probably central Asia	Palearctic, mostly 40–55°N, from central Europe discontinuously east to China[8a]	Africa, south-eastern Asia, and northern Australia[8b]	42 (22–26 January)
	Wood sandpiper *Tringa glareola*	Eastern Europe and western Asia	Forest tundra and taiga from Iceland and Scotland across Eurasia to Kamchatka, Siberia[9a]	Throughout sub-Saharan Africa, peripherally around Arabian Peninsula, and from India subcontinent and south-eastern Asia to Australia[9b]	39 (7–11 January)
(c)	Diederik cuckoo *Chrysococcyx caprius*	Central Africa	Malawi, Zambia, Zimbabwe, Namibia, and South Africa[10a]	Low-latitude populations are resident around the equator[10b]	29 (18–22 November)
	Little swift *Apus affinis*	Unknown	South Africa[11a]	Eastern Maghreb (Tunisia)[11b]	29 (18–22 November)
	Greater striped swallow *Hirundo cucullata*	Possibly Angola, southern DRC*, and Zambia	Angola, central Namibia, eastern Botswana, Zimbabwe, western	Central Africa north to Northern Angola, probably mainly west of 25°E[12b]	33 (8–12 Dec)

Table 1 (continued)

Common name	Provenance	Breeding	Nonbreeding	$[P_{\mathrm{SH}}]_s$
		Swaziland, Lesotho, and South Africa[12a]		
Paradise flycatcher *Terpsiphone viridis*	Cameroon and DRC*	South African coastal strip from the Western Cape to Saint Lucia and then to northern KwaZulu-Natal. Also in northern and eastern Botswana, northern Namibia, southern Zimbabwe, and southern Mozambique[13a]	Tropical Africa, as far as 5°N in Cameroon and DRC*. Some winter in southern lowlands of Zimbabwe and middle Zambezi river valley[13b]	38 (2–6 January)
South African cliff swallow *Hirundo spilodera*	Thought to be DRC*	Breeding endemic to southern Africa. Core range in South Africa from Mpumalanga, Gauteng and eastern north-western Province south and west to western Kwazulu-Natal, interior of eastern Cape and south-eastern northern Cape[16a]	Mainly in western DRC*[14b]	38 (2–6 January)
White-rumped swift *Apus caffer*	Unknown, but thought to be central Africa	Southern Africa[15a]	Unknown, but presumably in equatorial Africa[15b]	33 (8–12 Dec)
Whitethroated swallow *Hirundo albigularis*	Thought to be Angola, Zambia and southern DRC*	South Africa (throughout except NW Cape), Lesotho, Swaziland, Botswana (west to ca 22 ° E), Zimbabwe (mainly on central plateau and in east), Mozambique, Malawi[16a]	Angola, Zambia, and southern DRC*[16b]	33 (8–12 Dec)

The known breeding and nonbreeding grounds for these species are listed. P_{SH} is the southern hemisphere pentade, which is defined in relation to Berthold's pentade P_B as $P_{\mathrm{SH}} = P_B + 36$ if $P_B < 37$, and $P_{\mathrm{SH}} = P_B - 37$ otherwise (Altwegg *et al.*, 2012). $[P_{\mathrm{SH}}]_s$ gives the 5-day interval at which we split the year between the arrival phase and departure phase. As the asymptote was always reached well before, and after this point, the exact choice had no effect on our results. By default $[P_{SH}]_{Asym_s} = 38$, which represents the southern mid-summer. The abundance asymptote is reached earlier or later for some species, in that case $[P_{SH}]_{Asym_s}$ was adapted. [1a](Cramp, 1985), [1b](Cramp, 1985; Brooke & Herroelen, 1988), [2a](Fry *et al.*, 2000), [2b](Curry-Lindahl, 1981; Pearson & Lack, 1992; Lefranc & Worfolk, 1997; Harris & Franklin, 2000), [3a](Cramp, 1993), [3b](Cramp, 1993; Urban *et al.*, 1997), [4a,4b](Snow & Perrins, 1998a), [5a](Urban *et al.*, 1997; Snow & Perrins, 1998b), [5b](Urban *et al.*, 1997), [6a](Tree, 2005), [6b](Cramp & Simmons, 1983), [7a,7b](Cramp & Simmons, 1983; Tree, 1985; Rogacheva, 1992; Underhill, 1997; Zöckler, 2002), [8a,8b](Cramp, 1985; Urban *et al.*, 1986; Williams & Underhill, 1997), [9a](Hockey & Douie, 1995), [9b](Cramp & Simmons, 1983), [10a,10b](Keith *et al.*, 1992), [11a,11b](Keith *et al.*, 1992), [12a](Keith *et al.*, 1992), [12b](Benson *et al.*, 1971; Keith *et al.*, 1992; Dean, 2000), [13a](Keith *et al.*, 1992), [13b](Benson, 1982; Keith *et al.*, 1992), [14a](Earlé, 1997), [14b](Turner & Rose, 1989), [15a](Cumming, 1952; Maclean, 1993; Herremans, 1994), [15b](Fry *et al.*, 1988; Brooke, 1997), [16a](Broekhuysen, 1974; Keith *et al.*, 1992; Earlé, 1997), [16b](Turner & Rose, 1989).

*DRC stands for the Democratic Republic of the Congo.

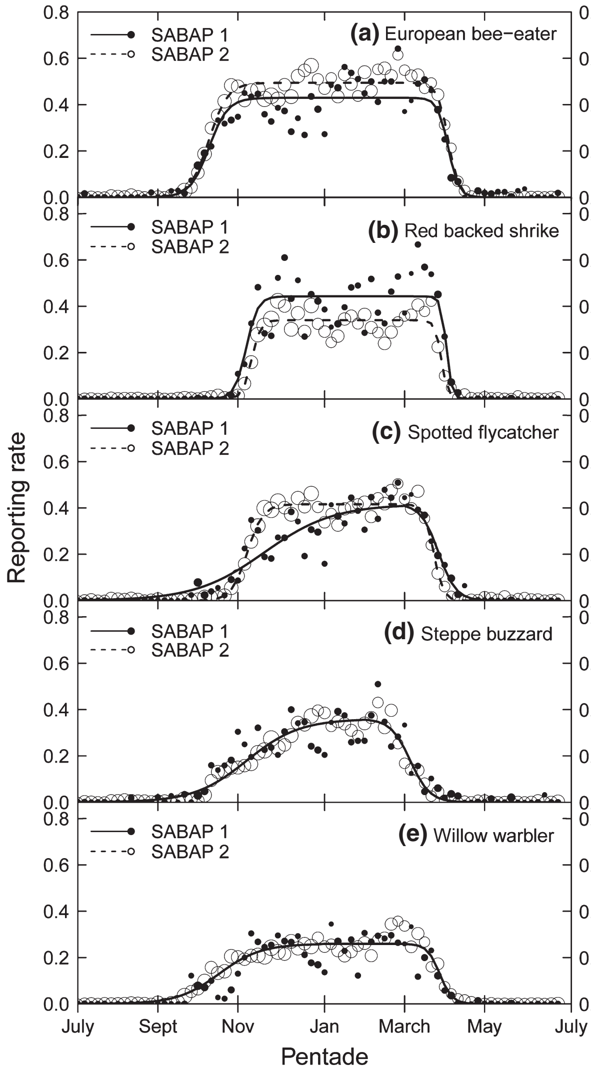

Fig. 1 The proportion of checklists recording each Palearctic migratory bird in the South African Highveld region throughout the year during 1987–1991 (SABAP1, solid line with filled circles) and 2007–2012 (SABAP2, dashed line with open circles): (a) European bee-eater, (b) red-backed shrike, (c) spotted flycatcher, (d) steppe buzzard, (e) willow warbler. 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 values (Table 3). The area of the symbols is proportional to the number of checklists, with the circles depicted in the legend representing 105 lists (same scale in all six panels).

the migrants leave again. As most species showed a long plateau of high reporting rates around $[P_{SH}]_s$, which is estimated by the parameter *Asym*$_s$, the exact choice of $[P_{SH}]_s$ had no effect on our results.

Extending the model, we then examined differences between the two atlas periods on phenology by making the parameters (e.g. the xmid_{a_s}) functions of a covariate (x_i, defining $x = -1$ for SABAP1 and $x = 1$ for SABAP2), where the coefficient β_0 estimates the mean across the two periods and β_1 estimates half the difference between SABAP1 and SABAP2:

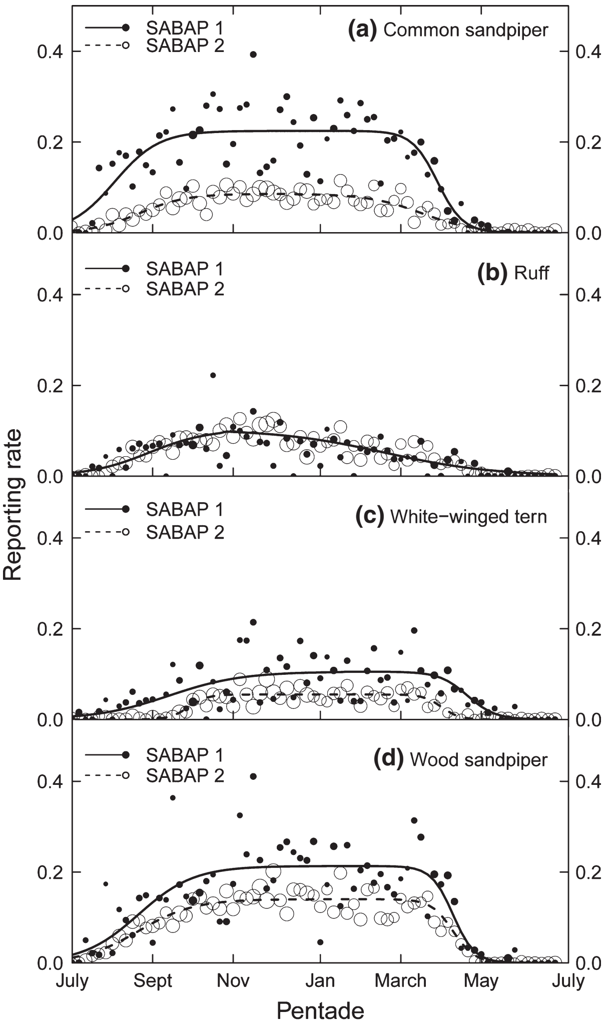

Fig. 2 The proportion of checklists recording each Palearctic waterbird in the South African Highveld region throughout the year during 1987–1991 (SABAP1, solid line with filled circles) and 2007–2012 (SABAP2, dashed line with open circles): (a) common sandpiper, (b) ruff, (c) white-winged tern, (d) wood sandpiper. See legend of Fig. 1 for more details.

$$\text{xmid}_{a_s} = \beta_0 + \beta_1 x_i \tag{2}$$

We considered eight variants of the basic model. Model 1 allowed all five parameters of equation (1) to differ between the two atlas periods (Table 2). Model 8 assumed all parameters to be equal between periods, that is β_1 is set to zero for all parameters. The other models represent a selection of possible combinations of variable arrival (described by the two parameters xmid_{a_s} and scal_{a_s}), departure (described by xmid_{d_s} and scal_{d_s}), and asymptote (Asym_s) across periods (Table 2). As we examine changes in the mean arrival and departure dates, our model does not confound phenological change with changes in abundance, in contrast to methods based on first and last detection data (Tryjanowski & Sparks, 2001).

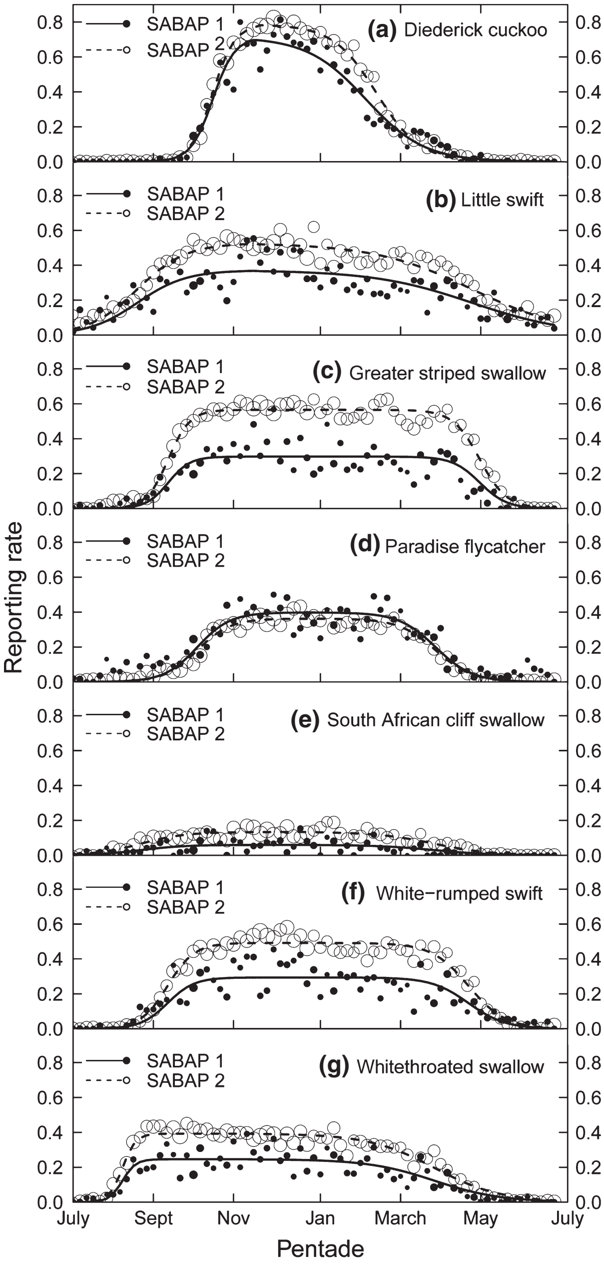

Fig. 3 The proportion of checklists recording each intra-African migratory bird in the South African Highveld region throughout the year during 1987–1991 and 2007–2012: (a) diederik cuckoo, (b) little swift, (c) greater striped swallow, (d) paradise flycatcher, (e) South African cliff swallow, (f) white-rumped swift, (g) whitethroated swallow. See legend of Fig. 1 for more details.

Table 2 Double-sigmoid curves fitted to Southern African Bird Atlas data to examine changes in migration phenology between the two project phases (1987–1991 and 2007–2012). The models contained five structural parameters (equation 1 in the text), the asymptote (Asym_s), mid-point and scale of arrival (xmid_{a_s} and scal_{a_s}), and mid-point and scale of departure (xmid_{d_s} and scal_{d_s}), which we allowed to vary between the two phases of the project ('×') or constrained to be the same ('–')

	Asymptote	Arrival		Departure	
	Asym_s	xmid_{a_s}	scal_{a_s}	xmid_{d_s}	scal_{d_s}
Model 1	×	×	×	×	×
Model 2	×	×	×	–	–
Model 3	×	–	–	×	×
Model 4	×	–	–	–	–
Model 5	–	×	×	×	×
Model 6	–	×	×	–	–
Model 7	–	–	–	×	×
Model 8	–	–	–	–	–

We then used Akaike's Information Criterion (AIC) to rank these models based on the difference in AIC between each model and the best model in the set [ΔAIC, (Burnham & Anderson, 2002)]. We also calculated Akaike weights (*w*), which estimate the relative support each model obtains from the data compared to the other candidate models (listed in Table 2). We used the model selection results in two ways. First, the ranking gave us an indication of which model (and corresponding hypothesis) was best supported by the data. Where the best model (with the highest AIC weight) was one of the six models allowing arrival and/or departure to vary (models 1, 2, 3, 5, 6, and 7, Table 2), we concluded that there was evidence for a change in phenology between the two atlas periods for the species in question. Second, we used the Akaike weights to calculate model-averaged estimates across all eight models and their unconditional confidence intervals (Burnham & Anderson, 2002) for all structural parameters and the changes between the two atlas periods.

Our main interest was in changes in phenology. We therefore further examined whether the change in the estimated mid-points of arrival and departure between the two atlas phases differed between the three groups of birds, Palearctic terrestrial migrants, Palearctic migratory waterbirds, and intra-African migrants. We analysed changes in arrival and departure separately in two Bayesian meta-analyses similar to that of McCarthy & Masters (2005) and Chambers *et al.* (2013). The basic structure of the model was similar to a regular linear model with change in mid-point of arrival and departure as response variables, group as a factor and normally distributed residuals. However, instead of treating the estimated phenology changes as observed without error, we modelled them as originating from a normal distribution using the model-averaged means and unconditional standard errors from the model selection analysis. We used noninformative priors ($N(0, 10^7)$ for the mean and differences among groups, and U(0,100) for the standard deviation of the residuals), and ran three Markov Chain Monte Carlo chains of 150 000 iterations, discarding the first 50 000 as burn-in. The Gelman-Rubin diagnostic indicated that these models converged quickly and all R-hat values were below 1.01. These analyses were carried out in program JAGS (Plummer, 2003) called from program R using the package 'rjags' (Plummer, 2014). The code is provided in the supplementary material (Appendix S1).

Table 3 Model selection analysis of migration phenology in South Africa for five Palearctic terrestrial migrants: European bee-eater, red-backed shrike, spotted flycatcher, steppe buzzard, and willow warbler

			European bee-eater		Red-backed shrike		Spotted flycatcher		Steppe buzzard		Willow warbler	
	Model	*K*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*
1	Asym. arrival. departure	11	4.72	0.04	*0*	*0.44*	2.33	0.19	4.72	0.03	6.59	0.01
2	Asym. arrival	9	1.81	0.19	2.78	0.11	6.72	0.02	0.25	0.30	3.92	0.06
3	Asym. departure	9	3.16	0.10	0.50	0.35	3.40	0.11	5.51	0.02	5.04	0.03
4	Asym	7	*0*	*0.47*	2.99	0.10	9.27	0.01	1.29	0.18	1.98	0.15
5	Arrival. departure	10	3.94	0.07	29.33	0	*0*	*0.61*	7.11	0.01	3.97	0.05
6	Arrival	8	3.26	0.09	35.58	0	4.43	0.07	2.93	0.08	1.54	0.18
7	Departure	8	6.85	0.02	32.69	0	14.80	0	4.18	0.04	2.44	0.12
8	None	6	6.12	0.02	38.84	0	18.88	0	*0*	*0.34*	*0*	*0.40*

The model column indicates which part(s) of the model was (were) allowed to vary between the two atlases (1987–1991 versus 2007–2012). 'Asym' refers to the asymptote (i.e. the maximum reporting rate). The term '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 mid-point 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.

Table 4 Model selection analysis of migration phenology in South Africa for four Palearctic migratory waterbirds: common sandpiper, ruff, white-winged tern, wood sandpiper

			Common sandpiper		Ruff		White-winged tern		Wood sandpiper	
	Model	*K*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*	ΔAIC	*w*
1	Asym. arrival. departure	11	*0*	*0.97*	6.80	0.01	*0*	*0.80*	4.20	0.06
2	Asym. arrival	9	7.43	0.02	3.45	0.06	5.94	0.04	3.02	0.11
3	Asym. departure	9	12.01	0	3.76	0.06	3.31	0.15	0.67	0.35
4	Asym	7	15.02	0	0.53	0.28	10.10	0.01	*0*	*0.49*
5	Arrival. departure	10	85.49	0	5.66	0.02	97.19	0	53.20	0
6	Arrival	8	221.46	0	3.90	0.05	50.79	0	45.83	0
7	Departure	8	265.07	0	1.77	0.15	47.46	0	47.02	0
8	None	6	308.82	0	*0*	*0.36*	52.11	0	47.25	0

See footnote of Table 3 for more details.

Results

Asymmetric phenology patterns

All studied species showed an asymmetric phenology pattern across the year with reporting rates for most species reaching a distinct plateau (an horizontal asymptote) in summer, when the species is most abundant (Figs 1–3). For all Palearctic migrants except the ruff–European bee-eater, red-backed shrike, spotted flycatcher, steppe buzzard, willow warbler, common sandpiper, white-winged tern, and wood sandpiper–the absolute value of the scale parameter for arrival was greater than the absolute value of the scale parameter for departure, $|\text{scale of arrival}| > |\text{scale of departure}|$, meaning that they arrived gradually and departed more rapidly (Tables A1 and A2 in Appendix S2). The seven intra-African migrants – diederik cuckoo, little swift, greater striped swallow, paradise flycatcher, southern African swallow, white-rumped swift, and white-throated swallow – and the ruff showed an asymmetric phenology pattern across the year opposite to the one shown by all other Palearctic migrants, that is $|\text{scale of arrival}| < |\text{scale of departure}|$ (Table A3 in Appendix S2).

Changes in maximum reporting rate

For 12 of the 16 species, the best model suggested a change in the maximum reporting rate between the

Table 5 Model selection analysis of migration phenology in South Africa for seven intra-African migratory birds: diederik cuckoo, little swift, greater striped swallow, paradise flycatcher, South African cliff swallow, white-rumped swift, and whitethroated swallow

			Diderick cuckoo		Little swift		Greater striped swallow		Paradise flycatcher		South African cliff swallow		White-rumped swift		Whitethroated swallow	
	Model	K	ΔAIC	w	ΔAIC	w	ΔAIC	w	ΔAIC	w	ΔAIC	w	ΔAIC	w	ΔAIC	w
1	Asym. arrival. departure	11	1.46	0.14	4.34	0.06	5.51	0.04	3.33	0.08	8.18	0.01	8.39	0.01	7.12	0.02
2	Asym. arrival	9	3.04	0.07	1.32	0.26	3.25	0.13	0.59	0.32	3.96	0.10	3.38	0.14	3.27	0.14
3	Asym. departure	9	*0*	*0.30*	4.46	0.05	2.34	0.20	2.82	0.11	4.00	0.10	5.13	0.06	3.69	0.11
4	Asym	7	0.97	0.18	*0*	*0.49*	*0*	*0.64*	*0*	*0.44*	*0*	*0.76*	*0*	*0.78*	*0*	*0.72*
5	Arrival. departure	10	0.28	0.26	2.51	0.14	20.33	0	5.94	0.02	7.27	0.02	12.37	0	13.11	0
6	Arrival	8	30.96	0	33.68	0	186.18	0	7.06	0.01	28.35	0	91.30	0	44.34	0
7	Departure	8	3.59	0.05	23.28	0	103.81	0	7.34	0.01	43.45	0	59.09	0	69.11	0
8	None	6	33.90	0	54.28	0	262.56	0	8.41	0.01	65.15	0	139.63	0	101.41	0

See footnote of Table 3 for more details.

two periods (Tables 3–5). For seven of them – the European bee-eater and six of the seven intra-African migrants (the exception was the paradise flycatcher) – the maximum reporting rates were higher in 2007–2012 than in 1987–1991. The greater striped swallow showed the greatest change; its maximum reporting rate increased by 0.27 between the two atlas periods, nearly doubling it (Table A3 in Appendix S2). The maximum reporting rates decreased in the other five species, three of the Palearctic migratory waterbirds (white-winged tern, common sandpiper, and wood sandpiper), plus red-backed shrike, and paradise flycatcher.

Changes in temporal migration patterns

For five of the 16 species (red-backed shrike, spotted flycatcher, common sandpiper, white-winged tern, and diederik cuckoo), the best model suggested a change in phenology between the two periods (Tables 3–5). In four further species (steppe buzzard, wood sandpiper, little swift, and paradise flycatcher), a model allowing for phenological changes ranked a close second best.

Next, we examined the changes in mean arrival and departure times, measured by the difference in the inflection point parameters (xmid) of the model (equation 1). Changes in arrival and departure times tended to be negatively correlated across species, that is species that delayed their arrival tended to advance their departure and vice versa (Fig. 4). The results are given in pentades as well as in days per year (d per yr); with 20.5 years separating the two central dates of the two atlas periods. The results for the five species for which the best model suggested phenological shifts are given in Table 6. The meta-analysis of the species–specific changes in arrival showed that the Palearctic terrestrial migrants on average advanced their arrival by −0.19 (95% credible interval −1.02 to 0.57) pentades ($-0.05\ \mathrm{d\ yr}^{-1}$), Palearctic migratory waterbirds delayed their arrival 0.36 (−0.44 to 1.36) pentades ($0.09\ \mathrm{d\ yr}^{-1}$), and the difference in mean arrival of intra-African migrants between the two periods was 0.01 (−0.47 to 0.50) pentades ($0.00\ \mathrm{d\ yr}^{-1}$). For all groups, the 95% credible interval included zero and there was therefore no clear evidence for a change in mean arrival date.

The meta-analysis of the species–specific change in departure showed that Palearctic migrants on average advanced their departure from South Africa by −0.68 (−1.30 to −0.04) pentades ($-0.17\ \mathrm{d\ yr}^{-1}$). This was mainly because the Palearctic migratory waterbirds advanced their departure by −1.25 (−2.44 to −0.02) pentades ($-0.30\ \mathrm{d\ yr}^{-1}$). For Palearctic

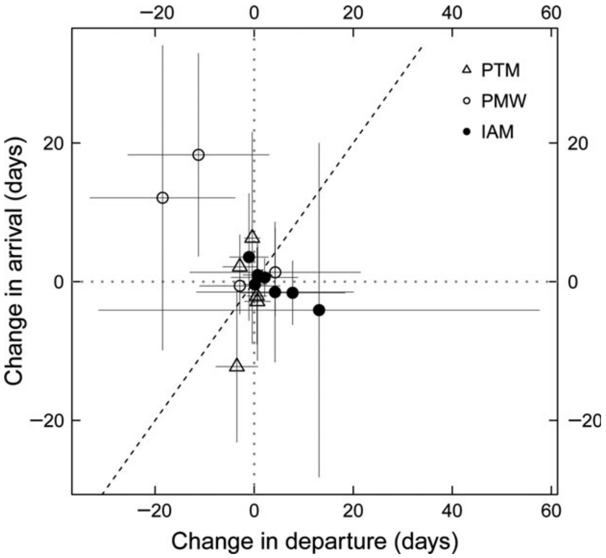

Fig. 4 Changes in arrival and departure of migratory birds in South Africa. 'PTM' stands for Palearctic terrestrial migrants, 'PMW' for Palearctic migratory waterbirds, and 'IAM' for intra-African migrants. Positive values mean a delay from the first period (1987–1991) to the second (2007–2012), a negative value means advance over this time period. The plotted values are model-averaged changes in the mid-point of a logistic curve describing arrival and departure (equation 1 in the main text), and unconditional confidence intervals. The grey dashed line is the line where changes in arrival equal changes in departure. Species to the left of this line shortened their stay in South Africa. The horizontal and vertical grey dotted lines indicate lines of no change.

terrestrial migrants, the 95% credible interval included zero (−0.11, 95% CI −0.47 to 0.19, $-0.03\ \mathrm{d\ yr^{-1}}$). Intra-African migrants delayed departure by 0.12 (−0.28 to 0.57) pentades ($0.03\ \mathrm{d\ yr^{-1}}$) but the 95% CI included zero.

Discussion

Examining shifts in migration phenology in a suite of species in the central Highveld of South Africa, we found that nearly a third of the species we considered have changed either their arrival date, departure date or both. The intra-African migrants we examined showed no clear patterns of change in their migration phenology. The clearest pattern emerged among Palearctic migrants that advanced departure from the study area between the periods 2007–2012 and 1987–1991. This advance was mainly driven by migratory waterbirds. Seasonal shifts in April temperature have been fastest in the high arctic (Burrows *et al.*, 2011) where most of the waterbirds in our sample breed. Red-backed shrikes and spotted flycatchers with a relatively northern breeding range were the two Palearctic terrestrial migrants that advanced their departure the most. These results are consistent with the hypothesis that climate change in the northern hemisphere breeding ranges is driving shifts in migration phenology of long-distance migrants and inconsistent with the hypothesis that migrants mainly time their departure in response to local conditions in South Africa. Under the latter hypothesis, we would expect all groups of migrants to show similar patterns. However, between-year variation might not be detected by our method and could still be explained by local conditions in South Africa. It is also possible for different species to be affected differently by the local conditions in South Africa, which would also lead to inconsistent patterns across species. The seasonal shifts in April temperature in South Africa have been relatively modest (Burrows *et al.*, 2011). However, seasonality in both April and October temperature has changed rapidly in the tropical regions of Africa. The fact that we did not see strong shifts in migration phenology of intra-African migrants could

Table 6 Difference in time of arrival and departure in the South African Highveld region, expressed in days, between 1987–1991 and 2007–2012 for the three different groups of species, and for the five species for which the best model suggested a changed phenology

		Arrival		Departure	
	Species	Earlier	Later	Earlier	Later
(a)	Red-backed shrike		2.15 (2.36) [0.10]	2.90 (1.76) [0.14]	
	Spotted flycatcher	12.25 (5.56) [0.59]		3.50 (2.15) [0.17]	
(b)	Common sandpiper		18.30 (7.47) [0.89]	11.25 (7.28) [0.55]	
	White-winged tern		12.10 (11.21) [0.59]	18.50 (7.49) [0.90]	
(c)	Diederik cuckoo				7.75 (5.41) [0.38]

Earlier and Later refer to the situation in 2007–2012 when compared with 1987–1991. The standard error is given in brackets. The shift in number of days per year is given in square brackets (it is a 20.5 year period between the two central dates of the two atlas periods). Results for the three different groups of birds are presented: (a) Palearctic terrestrial migrants, (b) Palearctic waterbirds, (c) intra-African migrants.

mean that their phenology is more driven by seasonality in their South African breeding range than by changes in their tropical African nonbreeding range.

Advanced departure could be a mechanism by which birds achieve an earlier return to the breeding grounds, which many species have been observed to do (Parmesan & Yohe, 2003; Root *et al.*, 2003; Knudsen *et al.*, 2011), including some of the species studied in this survey such as the spotted flycatcher and the red-backed shrike (Jonzen *et al.*, 2006). However, long-distance migrants also adjust their migration to environmental conditions along their migration route and the connection between timing of departure in South Africa and arrival at the northern hemisphere breeding site may not be straightforward. For example, Tøttrup *et al.* (2008) found that several long-distance migrants delayed prebreeding migration through the eastern flyway because of improved environmental conditions en route. However, except for willow warblers, the species they studied rarely migrate as far south as South Africa and the willow warbler was one of the species for which we did not detect a change in phenology. Studies in the northern hemisphere showed an advance of spring arrival dates for the willow warbler in Israel (Tøttrup *et al.*, 2008), Italy (Jonzen *et al.*, 2006), Germany and Denmark (Thorup *et al.*, 2007). This lack of correspondence between the shift in spring departure dates and the shift in spring arrival dates for the willow warbler could be due to accelerated migration en route, or the sampling of different populations showing different migrating patterns. Jenni & Kéry (2003) showed that long-distance migrants coming from the western half of Europe and heading for the Mediterranean basin and the Sahel in western Africa tend to leave Europe earlier after the breeding season. However, except for the spotted flycatcher, all Palearctic migrants we examined either delayed or did not change their arrival in South Africa, suggesting that they either spend more time migrating south or that long-distant migrants coming from eastern Europe and western Asia do not tend to leave earlier after the breeding season.

Our analysis revealed interesting asymmetric phenology patterns across the suite of species we examined. Most Palearctic species arrived gradually in their South African nonbreeding grounds and left South Africa more rapidly to reach their breeding grounds in the northern hemisphere. This could be caused by variation among individuals in the timing of departure after the breeding season (which could be explained by age-specific differences in migration phenology) or variation in the speed of migration, whereas there appeared to be less variation among individuals in their timing to leave the nonbreeding grounds. Intra-African migrants tended to show the opposite phenology pattern with rapid arrival and more gradual departure. As these species all breed in South Africa, the patterns are consistent with those found for Palearctic migrant and suggest more inter-individual variability in the timing of the postbreeding migration than in the timing of the prebreeding migration.

The analysis also showed substantial changes in maximum reporting rate between the two atlases for most of the studied species. Most Palearctic migratory waterbirds showed a substantial decrease in maximum reporting rate between the two atlases, whereas most of the intra-African migrants showed a substantial increase. Changes in maximum reporting rates for Palearctic terrestrial migrants were less consistent among species. Reporting rates can be interpreted as a measure of abundance (Robertson *et al.*, 1995; Huntley *et al.*, 2012), and the declining reporting rates for waterbirds is consistent with the reported decline of waterbird populations globally (Wetlands International, 2014). However, there is a comprehensive discussion of the caveats to the interpretation of reporting rate as a proxy for abundance in Harrison & Underhill (1997). We also caution against interpreting the observed changes in maximum reporting rates between the two atlases as changes in abundance because the spatial resolution at which data were collected changed between the two atlas projects. For SAPAB1, the cells in which the bird inventories were conducted were 15′×15′, whereas they were reduced to 5′×5′ for SABAP2. This might have altered the overall reporting rate of certain species due to dilution of the data, especially habitat specialists like waterbirds. Loftie-Eaton (2014) discussed the problems with the interpretation of reporting rates between the two atlas projects introduced by the change of size of grid cells.

Our method for studying migration phenology relies on data collected throughout the year and is therefore less sensitive to trends in observation effort than, for example, recording first or last observations of the season. In fact, first and last observations would not have been informative in our case because Palearctic migrants can skip a breeding season and remain in South Africa throughout the year (Harrison *et al.*, 1997a,b). Similarly, first and last observations would not be informative where individuals can spend the winter at their breeding grounds. Our method, on the other hand, can be used to examine phenology in such situations, extending ideas of using atlas data to study bird movement (Underhill *et al.*, 1992; Griffioen & Clarke, 2002). All species we examined left our study area almost completely but the model could easily be adjusted to situations where a considerable proportion of birds are resident. In that case, an additive term could be added to equation 1 to estimate the baseline reporting rate during the season when the species is least common. However, one drawback of using bird atlas data (and first/last observation data, for example) to study migration phenology is that they do not provide any information on the composition of the observed population. In our case, in particular, we cannot distinguish whether the observed phenology shifts were due to an overall shift in the entire population or whether the proportion of birds from different origins changed over time. For example, among the Palearctic migrants, populations breeding at different latitudes differ in their phenology (Both, 2010), and the observed phenology changes could in part be due to an increasing proportion of birds from populations that migrate earlier.

Our analysis of migration phenology of three groups of migratory birds in the South African Highveld showed clear patterns. The majority of the Palearctic migrants that changed their phenology shortened their stay at their South African nonbreeding grounds whereas intra-African migrants either showed no change or the changes were inconsistent among species. These patterns suggest that changes in the northern hemisphere conditions are a main driver for migration phenology in the South African bird community. Local conditions in South Africa or the tropical nonbreeding locations of the intra-African migrants did not appear to leave consistent traces in our data. Our results contrast with a recent comprehensive review of phenological changes across the southern hemisphere that found changes to be of similar magnitude to those observed in the northern hemisphere (Chambers *et al*., 2013). However, Chambers *et al.* (2013) highlight the lack of studies from tropical regions and Africa, a critical gap that our study is beginning to fill.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. BUGS code implementing the Bayesian meta-analysis for changes in phenology.
Appendix S2. Tables with parameter estimates.
Table A1. Parameter estimates for nonlinear regression models fitted to Southern African Bird Atlas Projects' records of five Palearctic terrestrial migrants: European bee-eater, red-backed shrike, spotted flycatcher, steppe buzzard and willow warbler.
Table A2. Parameter estimates for nonlinear regression models fitted to Southern African Bird Atlas Projects' records of four Palearctic migratory waterbirds: common sandpiper, ruff, white-winged tern and wood sandpiper.
Table A3. Parameter estimates for nonlinear regression models fitted to Southern African Bird Atlas Projects' records of seven intra-African migratory birds: diederik cuckoo, little swift, greater striped swallow, paradise flycatcher, South African cliff swallow, white-rumped swift and whitethroated swallow.