

Climatic influences on survival of migratory African Reed Warblers *Acrocephalus baeticatus* in South Africa

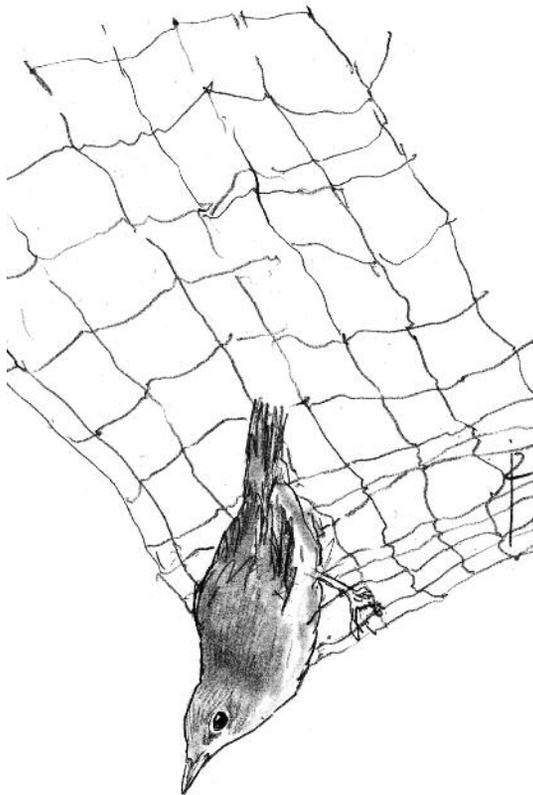
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Jansen D.Y.M., Wilson A.M. & Altwegg R. 2015. Climatic influences on survival of migratory African Reed Warblers *Acrocephalus baeticatus* in South Africa. *Ardea* 103: 163–174. doi:10.5253/arde.v103i2.a5

The focus of most research on the influence of recent climate change on birds has been on the northern hemisphere. Climate change has been different in the southern hemisphere, prohibiting extrapolation from northern research findings – and inference regarding future climate change – to species living there. We investigated the correlation between climatic conditions and survival of a migratory population of African Reed Warblers *Acrocephalus baeticatus* in Paarl, South Africa. We used temperature and rainfall in its breeding area, and Normalized Difference Vegetation Index (NDVI) in its wintering area, Central Africa around the Congo Basin. We fitted capture-mark-recapture models for open populations to a 12-year ringing dataset (1998–2010). After accounting for transience – this species exhibits high breeding site fidelity – with a 'Time-Since-Marking' model we found a mean survival probability of 0.79 ± 0.04 SE. Rainfall and NDVI did not influence survival in this dataset. Mean temperature (Aug–Apr) had a positive effect on survival: an increase of 1.6°C was associated with an increase of annual survival from 0.69 ± 0.05 to 0.88 ± 0.03 . Higher temperatures could have increased local survival by providing more food and breeding habitat, thereby increasing adult body condition and reducing foraging costs, predation and territorial conflicts. Even though we would need data on abundance and reproduction to quantify the effects of climatic conditions on population growth, we found a clear effect of climatic variation on a key demographic parameter, adult survival.

Key words: breeding area, capture-mark-recapture, Cormack–Jolly–Seber, environmental fluctuation, migration, Normalized Difference Vegetation Index, transience, wintering area

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The earth's surface was warmer in the past three decades than in any previous decade since 1850 (IPCC 2013). This period was likely the warmest in the past 1400 years in the Northern Hemisphere (IPCC 2014). Recent climate change has been linked to many different aspects of avian ecology and biology (see reviews by Parmesan 2006, Leech & Crick 2007, Travis *et al.* 2013). For species whose range is limited by climatic tolerance, a climate that moves outside that tolerance forces them to track their climate niche

(Peterson 2003). Tingley *et al.* (2009) compared century-old ranges with current ranges of 53 bird species in the Sierra Nevada mountains (California) and found that 48 species had moved following their climate niche in response to a warmer and wetter climate. In North America and Great Britain species with a southern breeding distribution have benefited from global warming, which allowed them to expand their ranges northward by an average of 60 km over 26 years (26 species) and 19 km over 20 years (59

species), respectively (Thomas & Lennon 1999, Hitch & Leberg 2007). Common breeding birds across Europe with little high temperature tolerance suffered population declines over 1980–2005, when the average temperature increased by 0.9°C (Jiguet *et al.* 2010). European migrants wintering in sub-Saharan Africa that have not advanced their arrival date at their breeding grounds, where springs have advanced over the past 50 years, have also decreased in abundance (Saino *et al.* 2011). Some species have shown enough phenotypic plasticity to adapt to recent climate change. A century ago White Stork *Ciconia ciconia* arrival on their breeding grounds differed per region in mountainous Slovakia, with earlier arrivals in warmer and lower regions (Gordo *et al.* 2013). Breeding success of early arrivals was higher than that of late arrivals. Since the late 1970s – after global warming commenced – spatial variation in arrival date mostly disappeared and breeding success no longer depends on timing, probably due to a more even spread of food supply over the breeding season (Gordo *et al.* 2013). In the UK sedentary Long-tailed Tits *Aegithalos caudatus* survived better in years with warmer springs and autumns – in four decades their population has more than doubled (Gullett *et al.* 2014).

Most studies of the impacts of recent climate change have focussed on the northern hemisphere, particularly on the northern, temperate region (Felton *et al.* 2009, Chambers *et al.* 2013, IPCC 2014, but see Kent *et al.* 2014). Since the northern hemisphere has warmed three times as fast over land as the southern hemisphere (IPCC 2007), gathered inference cannot easily be extrapolated to the southern hemisphere (Chambers *et al.* 2013). Globally the warming trend will likely continue in the first half of this century, and the probability increases to 'virtually certain' for the latter part of the century (IPCC 2013). The most conservative scenarios predict a global increase of at least 1.5°C by the end of the century (IPCC 2014). Confidence in the forecasts regarding changes in drought conditions and precipitation amounts and frequency is lower and varies per region. Climate change forecasts predict that regions in the southern hemisphere will experience extreme temperatures at a lower overall increase in temperature than the northern hemisphere, i.e. at an earlier stage of the forecasted global warming, and these will lead to more evaporation than identical increases in temperature in the northern hemisphere (Beaumont *et al.* 2011, Sherwood & Fu 2014).

To assess the impacts of future climate change on species and individual populations we need to deter-

mine the effect(s) of climatic conditions on demography (Robinson *et al.* 2007). The effects can be complex. Herfindal *et al.* (2015) found that warmer Aprils increased breeding success of female Goshawks *Accipiter gentilis* in Denmark, but negatively affected life-time reproductive success of the female's hatchlings of those years. Easier breeding conditions would also allow lower quality females to breed, which might have introduced an inferior component to that year's cohort (with poorer hunting skills).

Apart from reproduction and dispersal, the other key demographic parameter that influences population size is survival (Baillie & Schaub 2009). In the Arctic, warmer sea surface temperatures were negatively correlated with survival in three colonies of Little Auks *Alle alle* (Hovinen *et al.* 2014). This effect, with a time lag of one and two years, was likely caused through a lower food supply of lesser quality. Determining the factors that influence survival is more complex for migratory birds, because migrants are exposed to environmental conditions in their breeding area, during migration in flight and at stop-over sites, and in their wintering area (Newton 2004). In the UK, survival of Sedge Warblers *Acrocephalus schoenobaenus* was strongly correlated with rainfall in their Sahelian wintering grounds (Peach *et al.* 1991), but survival of Eurasian Reed Warblers *Acrocephalus scirpaceus* was not (Thaxter *et al.* 2006). Nonetheless, Ockendon *et al.* (2014) found that rainfall in the Sahel did have a strong impact on the abundance of both species.

With this study we aim to add to the evidence of the impacts of climate change on birds in the southern hemisphere. We investigated the correlation of survival of a migratory population of the African Reed Warbler *Acrocephalus baeticatus* with climatic conditions in the breeding area in South Africa and the wintering area in Central Africa. Since the 1950s temperatures have been rising across South Africa (Kruger & Shongwe 2004, Midgley *et al.* 2011), particularly in the Western Cape (Warburton *et al.* 2005), and the dry periods have become longer and more intense (Kusangaya *et al.* 2014). This warming trend is predicted to continue: until 2050 by 1–2°C in the coastal areas and 3–4°C in the interior, after 2050 by 3–4°C in the coastal areas and 6–7°C in the interior (Midgley *et al.* 2011) affecting the western parts of southern Africa most rapidly (Midgley *et al.* 2003). Precipitation is forecasted to decrease in the southwest of South Africa (Niang *et al.* 2014). In Central Africa the changes in mean annual temperature are expected to be relatively smaller than the predicted average 2+°C over the entire continent by the middle of this century and 4+°C by the end of



Adult African Reed Warbler caught and ringed in South Africa (Photo Dieter Oschadleus).

the century (Niang *et al.* 2014). For some regions in Central Africa with sufficient data over 1986–2005 to serve as baseline precipitation is forecasted to increase from the mid-21st century onwards, but the different climate scenarios do not agree for many regions in this area (Niang *et al.* 2014).

The African Reed Warbler is a partial intra-African migrant that breeds in wetlands south of the Sahara (Urban *et al.* 1997). Populations below 26°S are migratory; they are thought to migrate to Central Africa during the austral winter (June–Aug; Dean 2005). During the breeding season the African Reed Warbler breeds and forages for insects in moist or wet habitat (Urban *et al.* 1997), but during the non-breeding season it is less dependent on water: it forages in thick patches of shrubs and grasses away from water (Harrison 1997). In South Africa the African Reed Warbler is relatively common and at present of no conservation concern (Dean 2005). However, the precarious state of South Africa's wetlands – 65% threatened and 48% critically endangered – combined with the forecasted increase in open water evaporation and duration of dry spells could drastically alter the status of this species in the 21st century (Midgley *et al.* 2011, Driver *et al.* 2012). An added factor could be deteriorating conditions in the wintering area due to the forecasted increase in temperature (Christensen *et al.* 2007).

The African Reed Warbler is closely related to the Eurasian Reed Warbler, or even conspecific depending on the method used to determine genetic distance (Fregin *et al.* 2009, 2012). These closely related reed warblers conform to global patterns of life history variation among birds (see Jansen *et al.* 2014) for a comparison of their published demographic rates): northern, temperate species generally have low survival and high reproductive success, while southern, temperate species exhibit the opposite with higher survival and smaller clutch sizes (Ghalambor & Martin 2001; an example of closely related New World warblers in Salgado-Ortiz *et al.* 2008). Eurasian Reed Warblers have increased their seasonal reproductive success in response to warmer springs by advancing their breeding phenology, thus lengthening their breeding season (Halupka *et al.* 2008). We investigated climatic effects on survival of their southern, temperate counterparts, the African Reed Warblers. We analysed a 12-year capture-mark-recapture dataset collected through a public ringing scheme at Paarl in the Western Cape of South Africa. In addition to temperature, we investigated a potential effect of rainfall on survival. Both climatic variables could impact survival indirectly via a direct effect on breeding sites (reed beds) and food supply (insect abundance). The peak of the rainfall at the breeding grounds occurs in June–Aug, when most birds are at their wintering grounds, and as such

may affect survival in the subsequent breeding season. We therefore not only considered effects of rainfall in the current breeding season (Aug–Apr; year t), but also in the previous season ($t-1$).

Rainfall and temperature data were not available for the wintering grounds in Central Africa. We used the Normalized Difference Vegetation Index (*NDVI*) instead. This index is a measure of net primary productivity – a higher value signifies a greener environment (Pettorelli *et al.* 2005). *NDVI* is strongly correlated with rainfall and to a lesser degree with temperature (Wang *et al.* 2001, Pettorelli 2012). *NDVI* is particularly useful when the wintering area is large and not clearly delineated by recaptures or recoveries (Thaxter *et al.* 2006, Balbontín *et al.* 2009) as is the case for the African Reed Warbler. Therefore, we used *NDVI* of areas around the Congo Basin as a proxy for climatic conditions in the wintering area hypothesizing that in years with greener (wetter) winters survival would be higher.

METHODS

Ringling data

Adult African Reed Warblers were captured in mist-nets by licensed ringers (citizen scientists) according to the South African Ringing Unit protocol (SAFRING; de Beer *et al.* 2001) in and around Paarl Bird Sanctuary, a sewage works of 45 ha situated in the Western Cape of South Africa (33°43'S, 18°58'E; Figure 1). In the 12-year period between 1998 and 2010, 851 birds were captured between August and the following April, yielding 263 recaptures. August was chosen as the beginning of a capture occasion, because reed warblers start arriving from their wintering grounds during August and September to breed in the south-western Cape; they remain in their breeding grounds until March/April (Hockey *et al.* 1989). The resighting data were pooled over Aug–Apr to estimate annual survival (Appendix 2).

Captured individuals were aged by the volunteers, but at present no comprehensive guide exists to age South African bird species (de Beer *et al.* 2001). Therefore, SAFRING deemed data pertaining to age classes other than adult not reliable enough for use. Too few individuals of this sexually monomorphic species were sexed for use in the survival analysis.

Conditions in the breeding area

Temperature and rainfall were used as indicators of the environmental conditions in the breeding area. Temperature and rainfall were obtained from the

weather station at Paarl via the Climate Systems Analysis Group, University of Cape Town. Millimetres of monthly rainfall were aggregated over Aug–Apr. Monthly mean temperatures (degrees Celsius) were averaged over Aug–Apr. The derived estimates were used as covariates in the estimation of survival (Figure 2A and 2B; Appendix 2).

Over the study period mean temperature (Aug–Apr) did not show a discernible trend (Pearson's product moment correlation: $r = -0.10$ (95% CI $-0.66-0.53$), $t_9 = -0.30$, $P = 0.77$). Rainfall did show a weak decreasing trend (Spearman's rank correlation test: $r_s = -0.45$, $S = 320$, $P = 0.16$).

Conditions in the wintering area

Given the uncertainty of the location of the wintering area in Central Africa, we selected three areas around the Congo Basin: East, South and West (Figure 1). Normalized Difference Vegetation Index (*NDVI*) was used as an indicator of environmental conditions in the wintering area. *NDVI* is a satellite-derived index of vegetation quality that uses the normalized difference between the near-infrared (*NIR*) and red (*RED*) wavelengths reflected from the Earth's surface:

$$NDVI = (NIR - RED)/(NIR + RED)$$

(see Pettorelli *et al.* 2005 for details). The values typically range from near zero (e.g. soil, dying vegetation) to 1 (green vegetation). We used the MODIS MOD13C2 *NDVI* product (monthly values per 0.05 degree grid cells), downloaded from the Land Processes Distributed Active Archive Centre (LP DAAC), located at the U.S. Geological Survey (USGS) Earth Resources and Science (EROS) Centre (lpdaac.usgs.gov). Monthly anomalies per land cell (monthly *NDVI* minus monthly *NDVI* mean of the entire study period) were calculated for each wintering season (May–July), then averaged per season per block. A positive anomaly indicated a wetter (greener) than average season, a negative anomaly a drier than average.

The derived anomalies were used as covariates in the estimation of survival (Figure 2C; Appendix 2). MODIS data were available from 2000, so we estimated survival for 1998–1999 independently using an extra parameter. We fitted the blocks (Figure 1) separately, because the mean annual *NDVI* anomalies of East and South of the Congo Basin (EOCB, SOCB) were weakly correlated with each other (Pearson's product moment correlation: $r = 0.65$ (95% CI $0.03-0.91$), $t_8 = 2.40$, $P = 0.04$), the other blocks were not correlated ($r \leq 0.45$, $P \geq 0.19$).

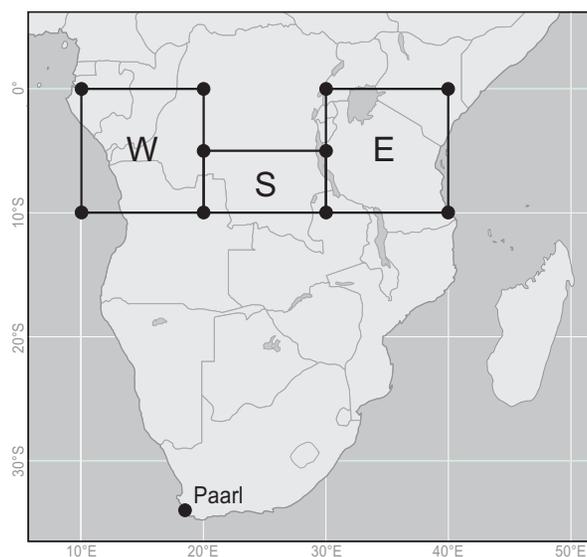


Figure 1. Capture location of the African Reed Warbler (Paarl) and its wintering area divided into three blocks in Central Africa: East (E), South (S) and West (W) of the Congo Basin. The decimal latitude and longitude of the north-west and south-east corner of each block were as follows: E 0.00°/10.00°, -9.83°/20.13°; S -4.50°/20.13°, -9.83°/30.28°; W 0.00°/30.28°, -9.83°/40.34°.

Capture-mark-recapture analyses

We used capture-mark-recapture models for open populations, which separate survival probability from recapture probability, to estimate apparent or local adult survival (hereafter survival) – 'apparent' because mortality cannot be separated from permanent emigration (Lebreton *et al.* 1992). To determine a general starting model that fitted the data a goodness-of-fit (GOF) test was performed of a Cormack–Jolly–Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) model with time-dependent survival (Φ) and recapture (p) ($\Phi(t)p(t)$) with program U-CARE 2.3.2 (Choquet *et al.* 2009). The overall GOF test was significant ($\chi^2_{32} = 56.04$, $P_{\text{two-tailed}} = 0.005$) as a result of the directional z -test for transience of Test3.SR ($z = 3.75$, $P_{\text{two-tailed}} = 0.0002$). The result indicated that more birds than expected were seen only once, which violates the assumption of the CJS model that every marked individual has the same recapture probability (Lebreton *et al.* 1992). Mist nets can only be placed at the edge of reed beds, where a territorial bird like the African Reed Warbler that nests safely away from the edge only occasionally forages (Urban *et al.* 1997, Eising *et al.* 2001). This behaviour could result in an overabundance of transients (Buckland & Baillie 1987). Passerine ringing data often show transience, i.e. non-local birds with an

apparent survival probability of zero after initial capture (Pradel *et al.* 1997). Not accounting for transience causes underestimation of survival for newly marked birds during the first period because that estimate is based on a mixture of transient and resident birds (Buckland & Baillie 1987).

Subsequently, we fitted a 'Time-Since-Marking' (TSM) model, in which initial capture is treated as a separate 'age' class from recapture ($a2$; Pradel *et al.* 1997). The transient effect was modelled as constant over time in $a2$, with time as an additive effect in $a2 + t$ and as an interactive effect in $a2 \times t$ ($= a2 + t + a2 \times t$). The median c-hat GOF, implemented in program MARK (White & Burnham 1999), was used to assess the fit of a TSM model with constant $a2$ survival and time-dependent recapture $\Phi(a2)p(t)$. Estimated c-hat for this model was 1.09 ± 0.04 SE (0.84–1.35) indicating no further evidence of overdispersion (Lebreton *et al.* 1992) and, therefore, an adequate representation of the structure in the data.

Program MARK 8.0 (White & Burnham 1999) was used for model fitting and R 3.1.1 (R Development Core Team 2014) for data handling, figures and statistical tests. We used simulated annealing to fit the more complex models and report profile likelihood confidence intervals. For the simpler models we used the faster standard Newton–Raphson algorithm after preliminary analyses showed that the two algorithms gave identical results. Corrected Akaike's Information Criterion ($AICc$) was used for model selection (Akaike 1973, Burnham & Anderson 2002). Estimates are shown with their standard errors.

RESULTS

Accounting for transience

To solve lack of fit we accounted for transience before considering climatic covariates. Models 6 and 7 (Figure 2D, Table 1) that accounted for transience showed a considerably better fit than model 9 – the corresponding model that did not account for transience ($\Delta AICc$; Table 1). The Time-Since-Marking (TSM) models with time-dependent (t) survival (models 7 and 10) showed parameter estimability problems (the number of estimated parameters was smaller than K in Table 1) due to sparseness of the data (low recapture probability). Model 6 with constant survival including a transient effect and time-dependent recapture was the most parsimonious model without covariates. Estimation of recapture of the last interval was problematic, even though it is theoretically estimable in these models due

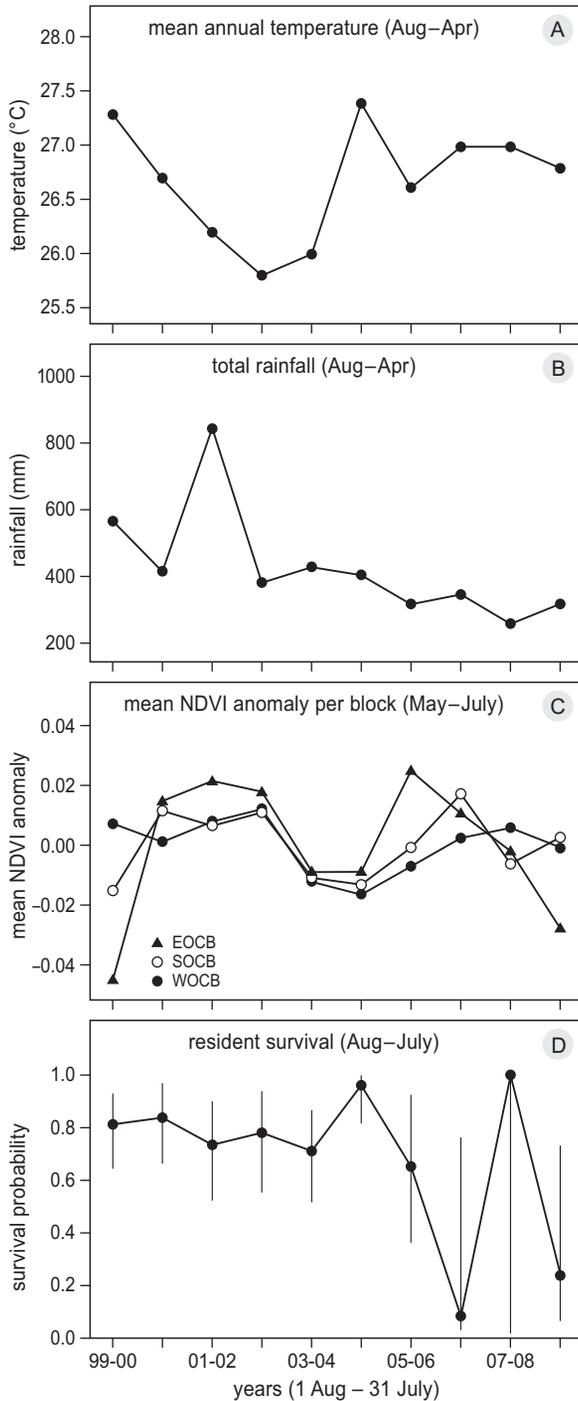


Figure 2. (A) Temperature, (B) rainfall (measured at Paarl, South Africa) and (C) NDVI values (1999–2009, for the three spatial blocks East, West and South of the Congo Basin (EOCB, WOCEB, SOCB) shown in Figure 1) used as covariates in model 1, 5, 2 to 4 and (D) annual resident survival (model 7, Table 1). Note that we could not separate resident from transient survival during the first year.

Table 1. Models fitted to African Reed Warbler ringing data (1998–2010) from Paarl.

| Model | $\Delta AICc$ | $AICc$ weight | K ‡ | Deviance |
|-------------------------------|---------------|---------------|-------|----------|
| 1. $\Phi(a2 + temp)p(t)$ § | 0.00 | 0.81 | 14 | 179.94 |
| 2. $\Phi(a2 + SOCB)p(t)$ | 6.18 | 0.04 | 15 | 184.06 |
| 3. $\Phi(a2 + EOCEB)p(t)$ | 6.23 | 0.04 | 15 | 184.11 |
| 4. $\Phi(a2 + WOCEB)p(t)$ | 6.69 | 0.03 | 15 | 184.58 |
| 5. $\Phi(a2 + rain)p(t)$ | 6.76 | 0.03 | 14 | 186.71 |
| 6. $\Phi(a2)p(t)$ | 6.94 | 0.03 | 13 | 188.94 |
| 7. $\Phi(a2 + t)p(t)$ | 7.96 | 0.02 | 23 | 169.20 |
| 8. $\Phi(a2 + rain prev)p(t)$ | 8.75 | 0.01 | 14 | 188.04 |
| 9. $\Phi(.)p(t)$ | 13.22 | 0.00 | 12 | 197.27 |
| 10. $\Phi(a2 \times t)p(t)$ | 14.47 | 0.00 | 31 | 158.79 |

$\Delta AICc$ = the difference with the smallest $AICc$; K = number of theoretically estimable parameters; Φ = survival probability; p = recapture probability; $a2$ = two Time-Since-Marking classes to account for transients; t = time-dependence; \times = interaction; $.$ = mean; $temp$ = mean temperature Aug–Apr; $SOCEB/EOCEB/WOCEB$ = mean NDVI anomaly May–July for south/east/west of the Congo Basin; $rain$ = total mm Aug–Apr; $prev$ = Aug–Apr of the previous year. § $AICc = 1272.74$. ‡ Models 2–4 have an extra parameter, compared to the other covariate models, estimating survival in 1998–1999 for which there was no NDVI data.

to the additive transients effect. However, estimability problems at the end of the study period are customary with sparse data (Lebreton *et al.* 1992). All models with a constant recapture probability were less well supported than models 1–10.

Model 6 estimated an initial survival (resident individuals + transients) probability of 0.51 ± 0.06 and a resident survival probability of 0.79 ± 0.04 . The proportion of residents was 0.65 (initial survival/resident survival; Pradel *et al.* 1997).

Environmental covariates

We then explored possible causes of temporal variation in survival, replacing the unconstrained time effect in model 7 by covariates: temperature (model 1, Table 1, Figure 2A; model 7, Figure 2D), Normalized Difference Vegetation Index (NDVI; models 2–4), rainfall (model 5), and rainfall over the previous year (model 8). Rainfall and mean temperature were not correlated (Spearman's rank correlation test: $r_s = -0.33$, $S = 292.16$, $P = 0.32$). Mean temperature (Aug–Apr) was not correlated with NDVI (May–July) of the Central African blocks ($r \leq -0.23$, $P \geq 0.13$) nor was rainfall ($r_s \leq 0.19$, $P \geq 0.61$).

Conditions in the breeding area

The model constraining survival to be a function of

temperature was clearly the best model in our set (model 1, Table 1), showing that annual variation in temperature (Aug–Apr) on the breeding grounds had a significant, positive influence on survival (Table 2). Temperature explained 46% of the temporal variation in survival (ANODEV $F_{1,9} = 7.54$, $P = 0.02$). Annual adult survival ranged from 0.69 ± 0.05 during August 2002 – July 2003, when mean temperature (Aug–Apr) was 25.8°C , to 0.88 ± 0.03 during 2004–2005, when mean temperature was 27.4°C (Figure 3). The unconstrained annual estimates from model 7 (Table 1) were less precise, but most 95% confidence intervals of model 1 fell within those of model 7 (Figure 3). The model with the temperature effect was 40 times more likely than the model with unconstrained temporal variation ($AICc$ weight model 1/ $AICc$ weight model 7 = $0.81/0.02$; Table 1).

Table 2. Covariate influence on annual adult survival.

| Covariate | Model (Table 1) | Regression Coefficient* | SE | 95% CI | |
|---------------|--------------------|----------------------------|-------|--------|-------|
| | | | | Lower | Upper |
| Temperature | 1 | 0.76 | 0.25 | 0.26 | 1.25 |
| SOCB | 2 | -17.60 | 17.61 | -52.10 | 16.91 |
| EOCB | 3 | -8.67 | 9.21 | -26.72 | 9.37 |
| WOCB | 4 | -13.03 | 18.79 | -49.86 | 23.81 |
| Rainfall | 5 | -0.002 | 0.001 | -0.004 | 0.000 |
| Rainfall prev | 8 | -0.002 | 0.001 | -0.003 | 0.002 |

For details of the covariates, see Table 1. *Slope on the logit scale.

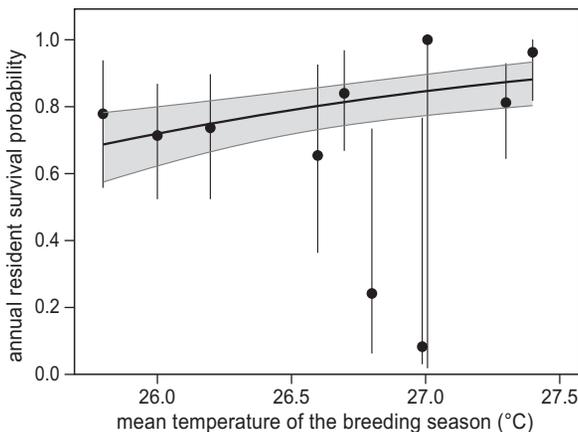


Figure 3. Apparent survival of adult African Reed Warblers in relation to temperature (Aug–Apr) at Paarl (1999–2010). The solid line shows the linear (on the logit scale) relationship between temperature and survival (model 1, Table 1). Grey lines show the 95% confidence interval. The points are the annual survival estimates from model $\Phi(a_2 + t)p(t)$ (model 7, Table 1, Figure 2D), the vertical lines their 95% profile likelihood confidence intervals.

Estimated recapture probabilities of model 1 ranged from 0.01 ± 0.009 for Aug–Apr 2007–2008 to 0.54 ± 0.09 during 1999–2000 (omitting 2009–2010 due to estimability problems; see Table A1 for all annual estimates and those of the additive time model 7).

Even though model 5 constraining survival to be a function of rainfall had a marginally lower $AICc$ value than the constant model (model 6), the confidence interval for the effect of rainfall included zero (Table 2) and there was therefore little evidence that annual variation in total rainfall during Aug–Apr had any influence on survival, nor of rainfall in the previous year (model 8; Table 2).

Conditions in the wintering area

We found no evidence that annual variation in $NDVI$ in the wintering area affected survival (all confidence intervals included zero; Table 2), as models 2 to 4 (Table 1) had only marginally lower $AICc$ values than the constant model (model 6). The lower $AICc$ value of the covariate models was mostly due to the fact that they estimated survival independently for the first year for which we had no $NDVI$ observations. The comparison of $AICc$ values therefore includes an element of unconstrained time variation for that year.

DISCUSSION

We found that annual apparent adult survival of the African Reed Warbler population in Paarl was significantly correlated with mean temperature (Aug–Apr) in the breeding area. When the temperature increased by 1.6°C , annual survival increased substantially by 0.19. The mechanism by which climatic conditions influence demographic parameters can be complex and indirect, and is often poorly understood (Gullett *et al.* 2014). For instance, when Gullett *et al.* (2014) linked higher temperatures to increased survival of Long-tailed Tits, direct higher mortality in less favourable weather appeared unlikely as none was observed. Instead, they suspected that severe conditions during breeding forced the parents to invest more in the nest, in foraging and in their own thermo-regulation leading to decreased body condition and, thus, eventually to higher mortality. This mechanism could also explain our findings: a temperature rise lead to increased food availability thus reducing foraging costs and a proliferation of reeds expanding the breeding habitat, thereby reducing territorial disputes and decreasing predation risk in denser and higher reeds (Urban *et al.* 1997, Eising *et al.* 2001, Leisler & Schulte-Hagen 2011). Another mechanism

could be increased local survival through reduced emigration: larger reed beds could reduce the need for breeding dispersal. However, as the African Reed Warbler exhibits high breeding site fidelity (Harrison 1997), this explanation appears unlikely.

The African Reed Warbler may initially profit from the forecasted increase in temperature in its breeding area, but the relationship between demography and climate is often non-linear (e.g. Nevoux *et al.* 2008). An increase larger than 1–2°C could well cause a decline in survival of the African Reed Warbler by drying out its breeding habitat. In The Netherlands declining water levels were found to decrease the abundance of water reeds (Graveland 1998).

Our mean adult survival estimate of the migratory African Reed Warbler in Paarl of 0.79 compared closely to the 0.77 estimated over 16 years for a sedentary population in Malawi (Peach *et al.* 2001). Thaxter *et al.* (2006) estimated 0.33 to 0.60 mean survival probability (1988–2004, range of two sites and sexes separately) for the closely related migratory Eurasian Reed Warbler in England. This considerable difference follows the generally accepted paradigm of the latitudinal gradient in survival, where northern, temperate passerines have a significantly lower survival rate than tropical and southern passerines (Martin 1996, Johnston *et al.* 1997, Peach *et al.* 2001, Leisler & Schulte-Hagen 2011 (reed warblers)).

Because of the limited duration of our study (10 annual resident survival estimates of which the last three were based on low recapture probabilities), the small sample size ($n = 851$), and the low number of recaptures ($n = 263$), we only considered models with a single environmental variable to avoid finding spurious relationships (overfitting; Young & Karr 2011). Using this approach, we were able to identify that mean temperature (Aug–Apr) in the breeding area was the only single variable that was significantly correlated with survival in this species. Rainfall over the current and previous year in the breeding area and *NDVI* in the wintering area were not significant predictors on their own, though it is quite possible that a larger dataset would allow exploration of more complex models and might reveal interacting effects of environmental conditions.

To accurately determine the influence of climatic conditions on population demography we need data pertaining to survival (here capture-mark-recapture data) as well as density (abundance data), fecundity and dispersal (Stenseth *et al.* 2004, Gullett *et al.* 2014). Regarding the latter, the African Reed Warbler has been observed as a cooperative breeder in a study area

where the habitat was saturated and dispersal opportunity was severely limited (Eising *et al.* 2001). Similarly, measures of food availability, predation risk, brood parasitism, habitat status and the impact of climate on these would enhance our understanding of what exactly influences which life history trait (see Jansen *et al.* 2014 for more detailed information regarding the African Reed Warbler; for other species, Foppen *et al.* 1999, Yom-Tov *et al.* 2006, Avilés *et al.* 2012). Data on all – or at least more – demographic parameters will also indicate which of the vital rates drive(s) population dynamics (Le Gouar *et al.* 2011, Robinson *et al.* 2012). In a developing country like South Africa, funding for data collection, let alone controlled experiments, is scarce. For most species, especially the common ones, the only data available are those collected by citizen scientists. The protocol for bird ringing could easily be expanded to include data collection of some of the aforementioned variables. However, fecundity and abundance data collection would need a rigorous protocol to ensure the safety of the study species and the reliability of the data.

ACKNOWLEDGEMENTS

We are grateful to the ringers, especially the late Gordon Scholtz, for collecting the data and to SAFRING for curating them. A.M.W. was supported by the NASA Earth and Space Science Fellowship Program (Grant NNX09AN82H). R.A. was supported by the National Research Foundation of South Africa (Grant 85802). The NRF accepts no liability for opinions, findings and conclusions or recommendations expressed in this publication.

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SAMENVATTING

Onderzoek naar de effecten van klimaatverandering op vogels is tot nu toe vooral op het noordelijk halfrond verricht. Omdat klimaatverandering zich op het zuidelijk halfrond anders ontwikkelt dan op het noordelijk halfrond kunnen de resultaten van onderzoek op het noordelijk halfrond niet zonder meer geëxtrapoleerd worden naar het zuidelijk halfrond en zijn voor-

spelingen over de effecten van klimaatverandering moeilijk te vertalen naar zuidelijke soorten. In dit artikel hebben we aan de hand van 12 jaar (1998–2010) vangst-merk-terugvangstgegevens in Zuid-Afrika gekeken naar het verband tussen klimatologische omstandigheden en de overleving van een populatie Kortvleugelkarekieten *Acrocephalus baeticatus* die vanuit het Zuid-Afrikaanse broedgebied aan het begin van de zuidelijke winter naar Centraal-Afrika (Congo-bekken) trekt om daar te overwinteren. De klimatologische factoren die we in beschouwing hebben genomen, zijn temperatuur en regenval in het broedgebied en een “Normalized Difference Vegetation Index” (*NDVI* of groenindex) in het overwinteringsgebied. Als we de lagere overleving in het eerste jaar na de vangst buiten beschouwing laten (mogelijk veroorzaakt door doortrekkers in de vangsten: broedvogels zijn in latere jaren zeer plaatstrouw aan hun broedgebied), is de gemiddelde jaarlijkse overleving $0,79 \pm 0,04$ (SE). Regenval in het broedgebied en de *NDVI* in het overwinteringsgebied hadden geen effect op de overleving, terwijl de gemiddelde temperatuur tijdens het broedseizoen (augustus–april) een positief effect had op de overleving. Een toename van $1,6^\circ\text{C}$ ging gepaard met een toename van de jaarlijkse overlevingskans van $0,69 \pm 0,05$ tot $0,88 \pm 0,03$. Hogere temperaturen leiden mogelijk tot een grotere beschikbaarheid van voedsel en broedhabitat, waardoor er minder lang gefoerageerd hoeft te worden, de vogels in betere conditie verkeren, en de kansen op predatie en territoriale conflicten kleiner zijn. Hoewel we aanvullende gegevens over aantallen en broedsucces nodig hebben om de effecten van klimatologische omstandigheden op de populatiegroei te kunnen bekijken, vinden we een duidelijk effect van klimatologische omstandigheden op een belangrijke demografische parameter, de overleving van volwassen vogels. (TL)

Corresponding editor: Tamar Lok

Received 18 January 2015; accepted 8 September 2015

APPENDIX 1.

Table A1. Annual recapture probability with 95% confidence intervals (model 1 and 7; Table 1).

| Capture occasion (Aug–Apr) | Recapture probability model 1 | 95% CI | | Recapture probability model 7 | 95% CI | |
|-------------------------------|-------------------------------------|--------|-------|-------------------------------------|--------|-------|
| | | Lower | Upper | | Lower | Upper |
| 1998–1999 | 0.54 | 0.36 | 0.71 | 0.54 | 0.35 | 0.73 |
| 2000–2001 | 0.14 | 0.08 | 0.23 | 0.15 | 0.08 | 0.26 |
| 2001–2002 | 0.15 | 0.09 | 0.24 | 0.16 | 0.09 | 0.27 |
| 2002–2003 | 0.17 | 0.10 | 0.28 | 0.16 | 0.09 | 0.27 |
| 2003–2004 | 0.17 | 0.10 | 0.28 | 0.16 | 0.09 | 0.27 |
| 2004–2005 | 0.22 | 0.14 | 0.32 | 0.18 | 0.11 | 0.25 |
| 2005–2006 | 0.21 | 0.14 | 0.32 | 0.24 | 0.11 | 0.46 |
| 2006–2007 | 0.08 | 0.04 | 0.14 | 1.00 | 0.08 | 1.00 |
| 2007–2008 | 0.01 | 0.00 | 0.05 | 0.02 | 0.00 | 1.00 |
| 2008–2009 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.22 |

APPENDIX 2.

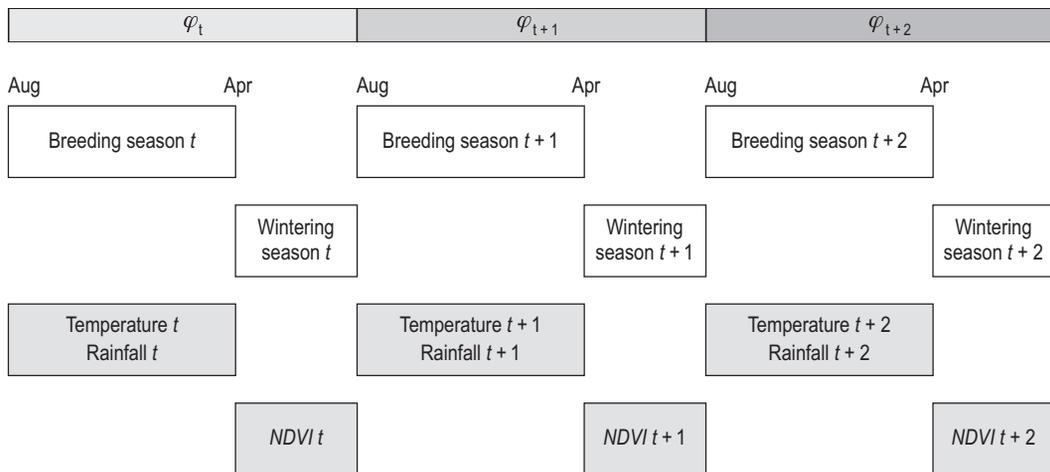


Figure A2. The timeline and intervals of the annual survival estimates and the covariates (light grey) used in the analysis of the capture-mark-recapture data of African Reed Warblers at Paarl (1998–2010).

Φ = survival probability; *NDVI* = Normalized Difference Vegetation Index