Climatic conditions during migration affect population size and arrival dates in an Afro-Palearctic migrant

Running title: *Climate and demography in Sand Martins*

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We would like to thank all members of the Lancaster and District Birdwatching Society who contributed sightings and Peter Cook for providing their data. Rob Robinson and Ian Hartley provided useful feedback on an earlier version of the manuscript, and Rob also advised on the statistical analyses. Thanks to the Editor, Associate Editor and anonymous reviewers whose comments helped to improve the manuscript.

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Article type : Short Communication

Editor : José Alves

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Long-distance migrants are particularly susceptible to climate change because of their multi-stage life-cycle but understanding how climatic conditions at each of these stages influence population dynamics remains a key challenge. Here, we use long-term data from a UK population of Sand Martins *Riparia riparia*, a declining Afro-Palearctic migrant, to investigate how weather on the wintering grounds and at passage sites impacts population size and arrival date. General linear models revealed that population size increased and arrival date advanced over the study period, and both were predicted by regional climatic variables in the previous winter and on passage. These results add to a growing body of evidence showing that population change in migrant birds is influenced by climatic conditions at all stages of the life cycle.

Key words: climate change, population dynamics, Sand Martin, *Riparia riparia*

In recent decades, Afro-Palearctic migrants have experienced significant population declines (Sanderson *et al.* 2006, Vickery *et al.* 2014) and shifts in phenology (Lehikoinen *et al.* 2004). Climate change is thought to have played a major role in driving these trends (Both & Visser 2001, Both *et al.* 2006, Sanderson *et al.* 2006), especially as long-distance migrants spend time in multiple regions and must cope with changing climatic conditions at each stage of their life cycle (Sillett *et al.* 2000, Both *et al.* 2009b, Jones & Cresswell 2010). Furthermore, conditions at one stage can influence populations later in the cycle (Gill *et al.* 2001, Newton 2004, Alves *et al.* 2012), although the fitness consequences of these 'carry-over effects' may not always be straightforward (Harrison *et al.* 2010, Senner *et al.* 2015). Most studies of how the climate impacts population dynamics in European migrants have focused on weather conditions on the wintering grounds (e.g. Baillie & Peach 1992, Robinson *et al.* 2008) or at various stages of spring migration through North Africa and Europe (e.g. Hüppop & Winkel 2006, Balbontin *et al.* 2009). However, further research is needed to understand how conditions at different stages interact to influence breeding population sizes and the timing of migration, especially in long-term studies of local populations (Gordo *et al.* 2013).

The major wintering area for many Afro-Palearctic migrants is the arid Sahel in Africa (Moreau 1972, Newton 2010). Population size and survival for these species is often positively correlated with Sahelian rainfall in the previous autumn (Sanderson *et al.* 2006, Robinson *et al.* 2008, Thaxter *et al.* 2010, Johnston *et al.* 2016), as these rains flood waterways for the winter and increase food availability (Peach *et al.* 1991, Cowley & Siriwardena 2005, Zwarts & van Horssen 2009). However, evidence also suggests that climatic factors during migration influence population size (Morrison *et al.* 2013), and that the weather conditions at stopover sites may be more important for survival than weather at the wintering grounds (Robinson *et al.* 2003, Schaub *et al.* 2005).

The timing of arrival of migrants at their breeding grounds can have important fitness consequences (Lozano *et al.* 1996, Alves *et al.* 2012), especially as arrival and breeding may be governed by both endogenous rhythms and environmental cues, causing phenological mismatches (Both & Visser 2001, Both *et al.* 2009a, Dunn & Møller 2014). Arrival dates for many species have advanced in recent decades (Lehikoinen *et al.* 2004, Sparks *et al.* 2007), most likely because climate change has shifted the timing of bud burst and insect emergence throughout migratory flyways (Marra *et al.* 2005, Gordo 2007). Although migrants are unlikely to be able to reliably predict conditions at breeding sites from the weather at the wintering grounds, it has been suggested that large-scale climate phenomena, such as the North Atlantic Oscillation (NAO), could provide environmental links between wintering, stopover and breeding sites. In years with high winter NAO values, conditions are warmer and wetter throughout continental Europe, but drier in southern Europe, causing earlier bud burst and insect emergence (Stenseth *et al.* 2003). This has been shown to correlate with the advanced arrival of migrants to their breeding grounds, either due to improved foraging or because conditions during northwards migrations act as cues to those on the breeding grounds (Forchhammer *et al.* 2002, Both *et al.* 2005, Rubolini *et al.* 2007). Indeed, it is unlikely that individuals respond directly to NAO values or air temperatures, but rather the effects these have on the ground and on body condition.

Sand Martins *Riparia riparia* are Afro-Palearctic migrants and a Species of European Conservation Concern (SPEC, BirdLife International 2004). While the UK population has shown signs of a recent increase, trends differ between regions (Morrison *et al.* 2013) and studies of local breeding populations may offer insights into the underlying mechanisms. Population size correlates strongly with Sahelian rainfall in the previous year (Szép 1995, Wernham *et al.* 2002, Zwarts & van Horssen 2009, Norman & Peach 2013), but no studies have investigated the effect of weather conditions during migration. Similarly, while the arrival dates of Sand Martins in the UK have advanced in recent years, and this has been linked to warmer spring temperatures (Mason 1995, Sparks *et al.* 2007), it remains unknown whether the conditions experienced during winter and migration influence arrival dates in local breeding populations. Here, we used general linear models to analyse long-term data on population size and arrival date from Lancashire, UK. We aim to investigate (1) how weather conditions at the wintering grounds and stopover sites affect local population size and arrival dates and (2) whether these conditions interact to mediate one another.

METHODS

Population size

The number of occupied Sand Martin burrows along an approximately 33 km stretch of the River Lune, Lancashire, UK, was counted every year from 1974 to 2014 using methods developed by the British Trust for Ornithology (BTO) for the Waterway Bird Survey (Williamson 1974, Marchant 1978). The site ranges from Skerton Weir near Lancaster

(54.06° N, 2.79° W) to Kirkby Lonsdale (54.2° N, 2.59° W), and the only year for which no data are available is 2001, when an outbreak of foot-and-mouth disease prevented access. Occupied burrows (i.e. nests) were counted in June, after most birds had started breeding but before most young had fledged, using binoculars to observe digging, repeated visits to the same burrow by adult birds and fresh droppings at burrow entrances; or by walking in front of the colony to observe birds leaving their burrows. The number of occupied burrows in each year was used as an estimate of population size; these methods have been shown to provide a reliable way of monitoring population change in this species (Norman & Peach 2013). Long stretches of river on either side of the study site are unsuitable for Sand Martins, but nesting habitat is not limiting within the site; changes in population size are therefore unlikely to be strongly influenced by density dependent breeding dispersal.

Arrival date

The first arrival dates of Sand Martins in Lancashire between 1957 and 2014 were provided by the Lancaster and District Bird Watching Society (LDBWS), who collate local records. However, fifteen years of data were missing during this period (1958-59, 1964, 1968-71, 1988 and 1992-1998) when no sightings away from breeding colonies were reported. Many records within the dataset came from RSPB Leighton Moss, a nearby nature reserve where daily bird observations have been recorded since 1966. In order to maximise the reliability of first arrival dates in Lancashire and to avoid missing years, the entire Leighton Moss dataset (from 1966 to 2014) and the LDBWS dataset were compared to find the earliest recorded arrival date in each year. First arrival dates, hereafter 'arrival dates', were taken to be the date of the first sighting anywhere in Lancashire, with only three years when no sightings were made (1958-59 and 1964). In years where sightings from both datasets were available, they were correlated at $r = 0.57$. Arrival dates are unlikely to accurately indicate the earliest arrival date of local breeders, especially as the earliest birds may not stay in Lancashire to breed but rather migrate further north (Sparks *et al*. 2005); observer effort may also have varied between years. Nonetheless, these sightings were considered to provide a useful index of the timing of arrival of Sand Martins in the Northwest of England.

Weather

The Sahel Rainfall Index between June and October was used as a measure of conditions in the subsequent winter. This is an index of the mean Sahelian rainfall across weather stations in the area bounded by 10°N–20°N and 20°W–10°E, provided by the Joint Institute for the

Study of the Atmosphere and Ocean (JISAO, http://research.jisao.washington.edu/data_sets/sahel/#analyses). The NAO Index for winter (December to March) was obtained from Hurrell (2015); this measures the difference in sea level pressure between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland, and is known to affect spring weather conditions in continental Europe (Hurrell 2015). Average monthly temperature and total rainfall across March and April in the area of North Africa bounded by 33° N–38° N and 9° W–12° E were obtained from the University of East Anglia Climatic Research Unit's (CRU) TS3.22 high-resolution gridded dataset (Jones & Harris 2008). This area is an important stopover site for Sand Martins and includes most ring recovery locations in North Africa, and these months were considered most biologically meaningful for the peak of passage through the region (Wernham *et al.* 2002, du Feu *et al.* 2009). Northwest English average monthly temperature and total rainfall in April and May, obtained from the Meteorological Office regional weather datasets (http://www.metoffice.gov.uk/climate/uk/summaries/datasets), were also collated because spring weather conditions are considered important correlates of arrival date in the UK (Wernham *et al.* 2002). Northwest England comprises South Cumbria, all of Lancashire, Greater Manchester, Merseyside and North Cheshire.

Statistical analysis

The effects of weather conditions on the wintering grounds and stopover sites on population size over a 40-year period were analysed using general linear models. Population size was fitted as the response variable, and predictors included the following: year of survey fitted as a continuous variable, the Sahel Rainfall Index in the previous year, the NAO Index in the previous winter and the North African average temperature (^{o}C) and total rainfall (in mm) in spring, together with the interactions between all pairs of weather variables. All two-way interactions were included because we wanted to investigate whether conditions at different stages had interdependent effects, but we had no clear predictions about which variables might be the most important (Saino & Ambrosini 2008). Northwest English weather data were not included because population size is more dependent on winter conditions than those immediately prior to arrival (Robinson *et al.* 2008). Year was included to account for any inter-annual variation in population size over and above that accounted for by the weather variables and to establish any temporal trends in population size over the study period. A change in conditions over time could also affect population size but including interaction terms between weather variables and year over-parameterised the models and reduced explanatory power.

Collinearity between all predictors was assessed using correlation plots and Variance Inflation Factors (VIFs, following Zuur *et al.* 2009). North African temperature and rainfall were highly negatively correlated (r=-0.7). North African temperature during spring is probably more important than rainfall due to its effects on photosynthesis and insect abundance (Both *et al.* 2005, Sparks *et al.* 2007, Robinson *et al.* 2008), and preliminary analyses showed that rainfall explained little additional variation in population size over and above temperature; only North African temperature was therefore included in the models. All the remaining variables were likely to have independent effects in the model (r<0.5 and VIFs <2 in all cases). All variables were centred and standardised (following Schielzeth 2010) before general least squares models in the *nlme* package were used to account for autocorrelation in population size between years (Pinheiro *et al.* 2015). The AR-1 autocorrelation structure, which implements greater similarity in population size in years close together than those further apart, was fitted to the data and compared to a general linear model (GLM) without autocorrelation. The GLM had a marginally lower AICc and was chosen over the autocorrelation model. GLMs were fitted in R version 3.2.3 (R Core Team 2019) with a Gaussian error distribution and the identity link function. All possible candidate models were fitted and compared using the AICc value; those within 2 AICc units of the best-fitting model were averaged in the *MuMIn* package (Bartoń 2015). Finally, model validation was carried out for the average model in order to verify that the best-fitting models were not violating assumptions. This was done by plotting the distribution of the model's residuals, the residuals versus fitted values and the residuals versus each explanatory variable.

The analysis of arrival dates in 54 years of records followed a similar procedure to that for population size. Arrival dates were converted into Julian Dates (JD, days since 1st January) and then fitted as the response variable in a GLM with the same explanatory variables as before, along with Northwest English temperature and rainfall (in April and May). The latter were considered likely correlates of arrival dates in Lancashire. Again, North African temperature and rainfall were highly correlated (r=-0.7), so rainfall was removed in subsequent analyses. Following this, the strongest correlations were found between Northwest English temperature and year, and North African temperature and year (r=0.5), whereas all others were weaker (r<0.5) and VIFs low (<2). All two-way interactions between weather variables were included and all variables were centred and standardised before analysis. The data were checked for autocorrelation using general least squares models as for the analysis of population size, but none was found. Therefore, GLMs were fitted with a Gaussian error distribution and identity link function, and then compared, averaged and validated using the same approach as above.

The data that support the findings of this study are available from the corresponding author upon reasonable request.

RESULTS

Population size

Population size along the River Lune showed marked fluctuations but a gradual increase over the study period (Fig. 1a). The variables Year, the Sahel Rainfall Index and North African temperature were present in the best-fitting models and were all positively correlated with population size (Table 1a, Online Supplementary Material Table S1, Fig. 1a, Fig. 2a, b). No other explanatory variables were in the top performing models.

Arrival date

The first arrival date of Sand Martins in Lancashire advanced over the study period (Fig. 1b). Arrival date was negatively correlated with year, the Sahel Rainfall Index and the NAO Index (Table 1b, Online Supplementary Material Table S2, Fig. 1a, Fig. 3a, b). Arrival date was also negatively correlated with North African temperature but positively correlated with Northwest English temperature, although the effect sizes were small (Table 1b). The effects sizes were also small for the interactions between the NAO Index and North African temperature, and between the NAO Index and Northwest English temperature (Table 1b).

DISCUSSION

The size of the River Lune Sand Martin population was positively correlated with the Sahel Rainfall Index in the previous year and North African spring temperature, even after controlling for inter-annual variation. This supports previous research showing that Sahelian rainfall influences population size in this and other species (Baillie & Peach 1992, Zwarts & van Horssen 2009, Norman & Peach 2013), but our results suggest that conditions at stopover sites are also important. Other studies have found that weather at stopover sites is crucial for migratory species and their population size, but primarily those species wintering in Southern Africa and using the Sahel as a stopover (Ebbinge & Spaans 1995, Newton 2006, Ockendon *et al.* 2014); ours demonstrates the impact of conditions in North Africa on population size in a European breeding population. For Sand Martins, like many species, crossing the Sahara Desert is very energetically costly, meaning that birds are likely to be in poor condition on arrival in North Africa (Balbontín *et al.* 2009). The stopover here allows migrants to increase their fat stores before continuing, but they may be particularly susceptible to changes in local weather at this time. Warmer temperatures may be important through their effect on photosynthesis and insect abundance (Berry & Bjorkman 1980, Bale *et al.* 2002, Sage & Kubien 2007) with increases in prey availability benefitting foraging efficiency and reducing competition, which may in turn improve survival during migration (Ebbinge & Spaans 1995, Morrison *et al.* 2007).

The arrival date of Sand Martins in Lancashire advanced over the study period and was negatively correlated with the Sahel Rainfall Index and the NAO Index. This suggests that improved conditions during winter and on migration resulted in earlier arrival in Lancashire, perhaps because such conditions allow birds to build up fat stores and complete their winter moult more quickly (Ebbinge & Spaans 1995, van den Brink *et al.* 2000). These findings contrast with those of Robson and Barriocanal (2011), who showed that favourable conditions at wintering grounds and stopover sites were associated with a delay in migration in various species. However, species respond differently to these conditions (Saino *et al.* 2007, Balbontín *et al.* 2009, Cooper *et al.* 2015), and some may even bypass certain stopover sites completely when the weather is favourable (Shamoun-Baranes *et al.* 2010). Alternatively, good conditions may increase the intra-individual spread in arrival dates to the breeding grounds, while delaying it on average. If so, first arrival date would not be representative of the population, although first arrival date is positively correlated with mean arrival date in many species (Sparks *et al.* 2005).

The NAO Index was strongly inverseley correlated with arrival date, as reported in other studies (Hüppop 2003, Rubolini *et al.* 2007). High NAO values in winter likely increase the speed of northward migration by improving conditions throughout Europe prior to arrival

(Stenseth *et al.* 2003, Rubolini *et al.* 2007). A high NAO also advances spring phenology, thereby facilitating an earlier start to the breeding season (Forchhammer *et al.* 1998, Hüppop 2003, Parmesan & Yohe 2003, Rubolini *et al.* 2007).

The effect of weather conditions in winter and on migration may not influence arrival dates through their impact on body condition, but rather by providing birds with cues to conditions on the breeding grounds. Studies of other species have found individuals to be highly repeatable in their migration schedule, particularly in their pre-breeding movements (Stanley *et al.* 2012, Conklin *et al.* 2013), and individuals may use weather conditions to inform migratory timing (Both 2010, Schmaljohann *et al.* 2012). Correlations between weather conditions at breeding and wintering sites are likely to provide cues for migratory birds to adjust their migration schedule (Saino & Ambrosini 2008), but their usefulness may be reduced due to the spatial variability of climate change (La Sorte *et al.* 2019). It is most likely that both body condition and the provision of cues influence arrival dates given that individuals may be repeatable in migration schedule but less so in the route taken, which is presumably dependent on ground conditions (Stanley *et al.* 2012).

It is likely that the weather variables we investigated are correlated with conditions elsewhere in the migratory flyway of Sand Martins (Saino & Ambrosini 2008). It is therefore difficult to know whether these variables are directly affecting individuals or if the weather elsewhere is more important. Regardless, they provide a useful index of the climatic conditions which affect migratory species. This study therefore reinforces the notion that climatic factors at all stages of migration are likely to be important determinants of population change for Afro-Palearctic migrants. While the interactions between the climatic variables were weak and there may not be carry-over effects between the conditions Sand Martins experience at different stages of migration, future studies of other species should also test for these effects. Understanding the influences of large-scale environmental processes and conditions on changes in local populations could provide valuable insights for migrant conservation and improve our predictions of how animal populations will respond to future climatic change.

We would like to thank all members of the Lancaster and District Birdwatching Society who contributed sightings and Peter Cook for providing their data. Rob Robinson and Ian Hartley provided useful feedback on an earlier version of the manuscript, and Rob also advised on the statistical analyses. Thanks to the Editor, Associate Editor and anonymous reviewers whose comments helped to improve the manuscript.

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TABLES

Table 1. The results of the GLMs investigating (a) the effects of climatic factors on population size in Sand Martins along the River Lune, Lancashire, UK (n = 39) and (b) the effects of climatic factors on arrival date to Lancashire, UK (n = 53). Only models within 2 AICc of the best-fitting model are presented here. Values are the parameter estimates for each variable (± standard error). Variable abbreviations are as follows: NAT = North African temperature, SRI = Sahel Rainfall Index, NER = Northwest English rainfall, NET = Northwest English temperature, AICc = Aikaike Information Criterion corrected for small sample size, ΔAICc = Difference in AICc between the i^{th} model and the best-fitting model, Weight = Normalised model likelihoods.

(a) Population size							
Model ID	**Intercept**	**NAT**	**SRI**	**Year**	**R^2**	**ΔAICc**	**Weight**
7	1388.15	235.95 (83.30)	305.36 (73.74)	-	0.44	0.00	0.24
15	1392.70	172.87 (93.67)	257.65 (84.8)	140.87 (100.29)	0.47	0.50	0.18
13	1389.47	-	251.98 (87.52)	229.62 (90.91)	0.42	1.48	0.11

(b) Arrival date											
Model ID	**Intercept**	**NET**	**NAT**	**NAO**	**SRI**	**Year**	**NET x NAO**	**NAT x NAO**	**R^2**	**ΔAICc**	**Weight**
57	76.08	-	-	-4.20 (0.96)	-1.65 (0.94)	-4.88 (0.97	-	-	0.52	0.00	0.03
36927	76.49	1.07 (1.03)	-1.17 (1.01)	-5.23 (0.97)	-1.76 (0.91)	-4.21 (1.21)	-2.28 (1.00)	2.59 (1.11)	0.61	0.26	0.02
41	76.13	-	-	-3.78 (0.95)	-	-4.76 (0.99)	-	-	0.49	0.81	0.02
36911	76.55	0.75	-1.42	-4.76	-	-3.83	-2.39	2.42	0.58	1.55	0.01

		(1.05)	(1.03)	(0.96)		(1.23)	(1.02)	(1.14)			
			-0.73	-4.46	-1.72	-3.99		1.95			
32829	76.00	-	(1.03)	(0.96)	(0.94)	(1.17)	-	(1.13)	0.55	1.55	0.01
		0.89		-4.70	-1.70	-5.38	-1.62				
4155	76.45	(1.07)	-	(0.99)	(0.94)	(1.11)	(1.00)	-	0.55	1.56	0.01
		0.92		-4.35	-1.80	-5.36					
59	76.11	(1.08)	-	(0.98)	(0.96)	(1.13)	-	-	0.53	1.76	0.01

FIGURE LEGENDS

Figure 1. (a) The population size of Sand Martins along the River Lune, Lancashire, UK, between 1974 and 2014 and (b) the arrival dates of Sand Martins in Lancashire, UK, between 1957 and 2014. Solid grey lines are the predicted relationships after models within 2 AICc of the best-fitting GLM were averaged, with all other variables kept at their mean value. Shaded areas show 95% confidence intervals

Figure 2. The relationships between the population size of Sand Martins along the River Lune, Lancashire, UK, and (a) the Sahel Rainfall Index during the previous winter, and (b) the NAO Index during the previous winter. Closed circles are raw data and lines show predicted relationships after models within 2 AICc of the best-fitting GLM were averaged, with all other variables kept at their mean value. Shaded areas show 95% confidence intervals.

Figure 3. The relationships between the arrival dates of Sand Martins in Lancashire, UK, and (a) the NAO Index during the previous winter and (b) Sahel Rainfall Index in June-October the previous year. Closed circles are raw data and lines show predicted relationships after models within 2 AICc of the best-fitting GLM were averaged, with all other variables kept at their mean value. Shaded areas show 95% confidence intervals.

FIGURES

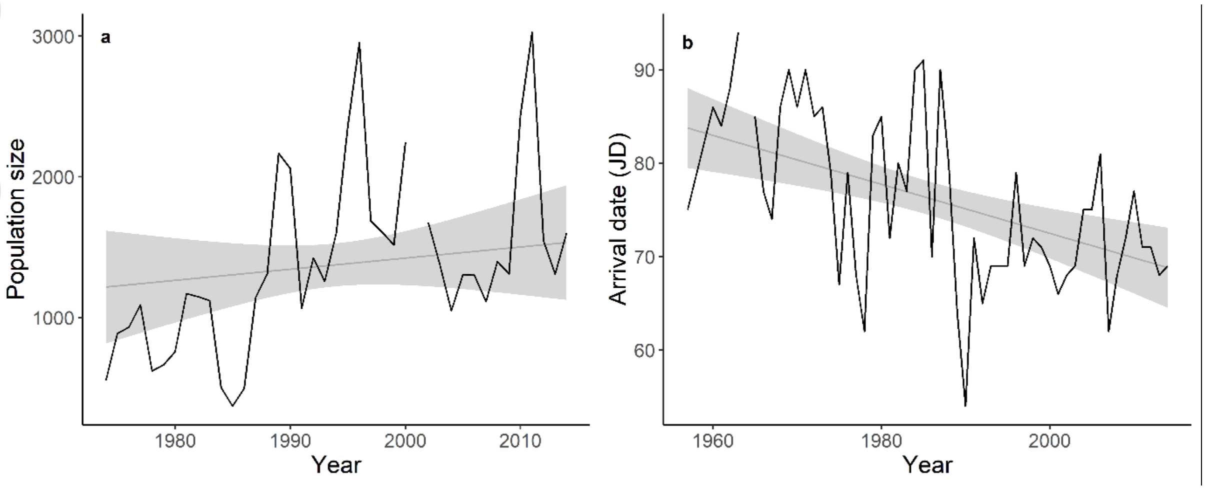

Figure 1

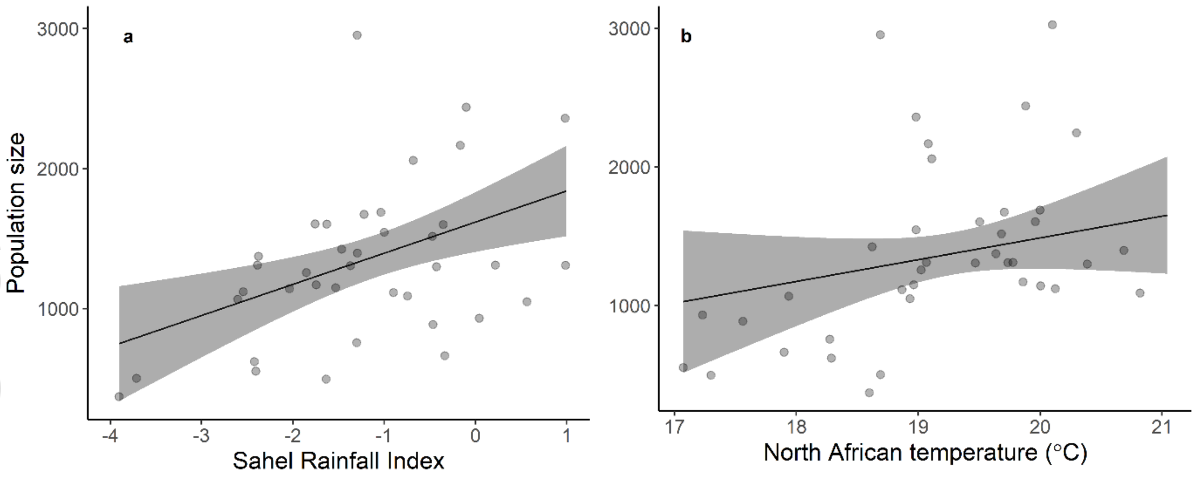

Figure 2

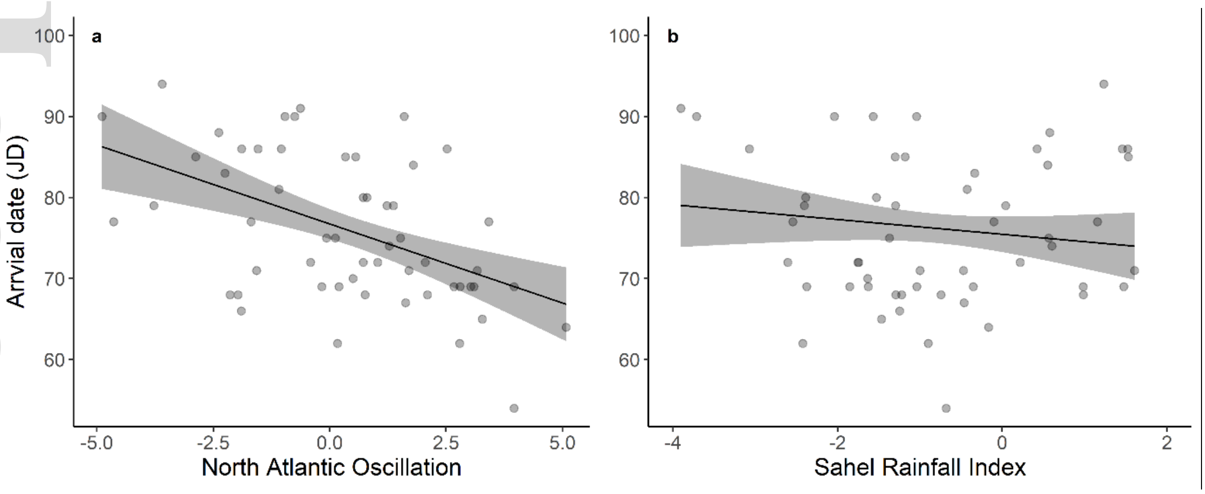

Figure 3

APPENDICES

Supplementary Online Material (SOM)

SOM Figure Legends

Table S1. The set of linear models (GLMs) within 5 AICc units of the best-fitting model of the correlates of the population size of Sand Martins on the River Lune, Lancashire, UK. Model averaging was carried out on the models within 2 AICc units of the best-fitting model; these are shown in bold. For the full set of GLMs contact the corresponding author. Int = Intercept, NAO = North Atlantic Oscillation Index, NAT = North African temperature, SRI = Sahel Rainfall Index, yr = year, AICc = Akaikes Information Criterion corrected for small sample sizes, delta = Difference in AICc between a given model and the best-fitting model, weight = The probability of any given model being the best-fitting model, the normalised relative likelihood.

Table S2. The set of general linear models (GLMs) within 5 AICc units of the best-fitting model of the correlates of the arrival dates of Sand Martins in Lancashire, UK. Model averaging was carried out on the models within 2 AICc units of the best-fitting model; these are shown in bold. For the full set of GLMs contact the corresponding author. Columns containing the two-way interactions between English Rainfall and English Temperature and English Rainfall and North African Temperature have been omitted because they appeared in none of models within 5 AICc units of the best-fitting model. Int = Intercept, NER = Northwest English rain, NET = Northwest English temperature, NAT = North African temperature, NAO = North Atlantic Oscillation Index, SRI = Sahel Rainfall Index, yr = Year, AICc = Akaikes Information Criterion corrected for small sample sizes, delta = Difference in AICc between a given model and the best fitting model, weight = The probability of any given model being the best-fitting model, the normalised relative likelihood.