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## Research

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### Author for correspondence:

James W. Pearce-Higgins

e-mail: [james.pearce-higgins@bto.org](mailto:james.pearce-higgins@bto.org)

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## Population ecology

# Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds

Nancy Ockendon, Dave Leech and James W. Pearce-Higgins

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

Long-distance migrants may be particularly vulnerable to climate change on both wintering and breeding grounds. However, the relative importance of climatic variables at different stages of the annual cycle is poorly understood, even in well-studied Palaearctic migrant species. Using a national dataset spanning 46 years, we investigate the impact of wintering ground precipitation and breeding ground temperature on breeding phenology and clutch size of 19 UK migrants. Although both spring temperature and arid zone precipitation were significantly correlated with laying date, the former accounted for 3.5 times more inter-annual variation. Neither climate variable strongly affected clutch size. Thus, although carry-over effects had some impact, they were weaker drivers of reproductive traits than conditions on the breeding grounds.

## 1. Introduction

Many long-distance Palaearctic migrant birds have undergone recent dramatic population declines [1], and may be particularly vulnerable to impacts of climate change, as they are affected by weather conditions at various locations throughout their annual cycle. Climate on wintering grounds has been demonstrated to affect overwinter survival of some species [2,3], while changes in abundance of other species have been attributed to climate change on breeding grounds [4].

There is increasing awareness of the potential for linkages between breeding and wintering ground conditions to affect migrant populations [5]. Carry-over effects can occur if wintering ground climate influences the condition of birds when they come to depart on spring migration, potentially altering arrival time on breeding grounds and affecting reproductive success [6–8]. A recent analysis demonstrated a correlation between precipitation on West African wintering grounds and mean laying date in seven out of 11 migrant bird species [9] but did not account for breeding conditions. The relative importance of breeding and wintering ground climate in determining reproductive phenology and output across species therefore remains unknown.

We attempt to disentangle these effects using a dataset of UK nest records from 19 species of Afro-Palaearctic migrant birds over a 46-year period. We quantify the relative importance of precipitation on African wintering grounds (which drives vegetation growth and resource availability) and UK spring temperature on two reproductive traits likely to reflect female condition at the start of the breeding season: date of initiation of laying and clutch size.

## 2. Material and methods

We investigated 19 long-distance migrant species where all (17 species) or a significant proportion (two species) of the UK population winters south of the Sahara [10]

**Table 1.** Species used in analysis, with wintering zones derived from literature and recoveries of ringed birds and mean annual values and sample sizes for nesting parameters. Secondary wintering zones are given in parentheses where there is uncertainty over classification [11]. An unknown proportion of common chiffchaff and Eurasian blackcap winter north of the Sahara desert (northern).

species	wintering zone	first egg date (days from 1 January)		clutch size	
		mean (s.e.)	<i>N</i>	mean (s.e.)	<i>N</i>
European turtle dove <i>Streptopelia turtur</i>	humid (arid)	167 (1.60)	12.2	1.96 (0.011)	11.3
sand martin <i>Riparia riparia</i>	arid	156 (3.90)	33.7	4.30 (0.16)	29.8
barn swallow <i>Hirundo rustica</i>	southern	169 (0.66)	200	4.52 (0.011)	454
wood warbler <i>Phylloscopus sibilatrix</i>	humid	143 (0.57)	34.2	5.71 (0.054)	18.3
common chiffchaff. <i>Phylloscopus collybita</i>	arid/northern	130 (0.97)	54.5	5.46 (0.026)	36.8
willow warbler <i>Phylloscopus trochilus</i>	humid	136 (0.50)	84.4	5.93 (0.026)	48.3
Eurasian blackcap <i>Sylvia atricapilla</i>	arid/northern	138 (0.92)	39.8	4.55 (0.017)	38.6
garden warbler <i>Sylvia borin</i>	humid	144 (0.69)	22.1	4.35 (0.033)	16.8
lesser whitethroat <i>Sylvia curruca</i>	arid	142 (0.75)	8.65	4.61 (0.056)	6.22
common whitethroat <i>Sylvia communis</i>	arid	147 (0.98)	20.1	4.68 (0.019)	31.0
sedge warbler <i>Acrocephalus schoenobaenus</i>	arid	148 (0.74)	47.0	5.02 (0.025)	34.9
Eurasian reed warbler <i>Acrocephalus scirpaceus</i>	humid (arid)	166 (0.79)	198	3.89 (0.013)	139
spotted flycatcher <i>Muscicapa striata</i>	humid	161 (0.43)	70.4	4.24 (0.014)	78.1
pie'd flycatcher <i>Ficedula hypoleuca</i>	humid	135 (0.62)	430	6.69 (0.034)	348
common redstart <i>Phoenicurus phoenicurus</i>	arid	137 (0.81)	62.7	6.21 (0.034)	49.0
whinchat <i>Saxicola rubetra</i>	humid	147 (0.52)	26.9	5.55 (0.051)	11.7
wheatear <i>Oenanthe oenanthe</i>	arid	136 (1.10)	13.7	5.37 (0.071)	11.2
yellow wagtail <i>Motacilla flava</i>	arid	147 (1.40)	5.86	5.14 (0.066)	5.38
tree pipit <i>Anthus trivialis</i>	humid	140 (0.79)	19.9	4.84 (0.055)	10.9

and sufficient nest record data exist (table 1). Following the methods of Crick *et al.* [12], clutch size and first egg date (FED) were extracted from the British Trust for Ornithology's Nest Record Scheme dataset (1966–2011). Clutch size was the maximum number of eggs recorded in a given nest across all visits. FED was calculated by relating information about nest contents to the length of different stages of the nesting cycle (see electronic supplementary material, appendix S1).

Nesting parameters were related to climatic conditions on species' sub-Saharan wintering grounds defined using known winter African distribution and recoveries of ringed birds [11] into the following zones (see electronic supplementary material, appendix S2):

- (i) *Arid*: 11° N–17° N, 17° W–13° E.
- (ii) *Humid*: 4° N–8° N, 15° W–9° E.
- (iii) *Southern*: 35° S–23° S, 17° E–33° E.

As most species that winter further south in Africa use the arid zone as a stopover point on northward migration [13], variables relating to this zone were tested across all species.

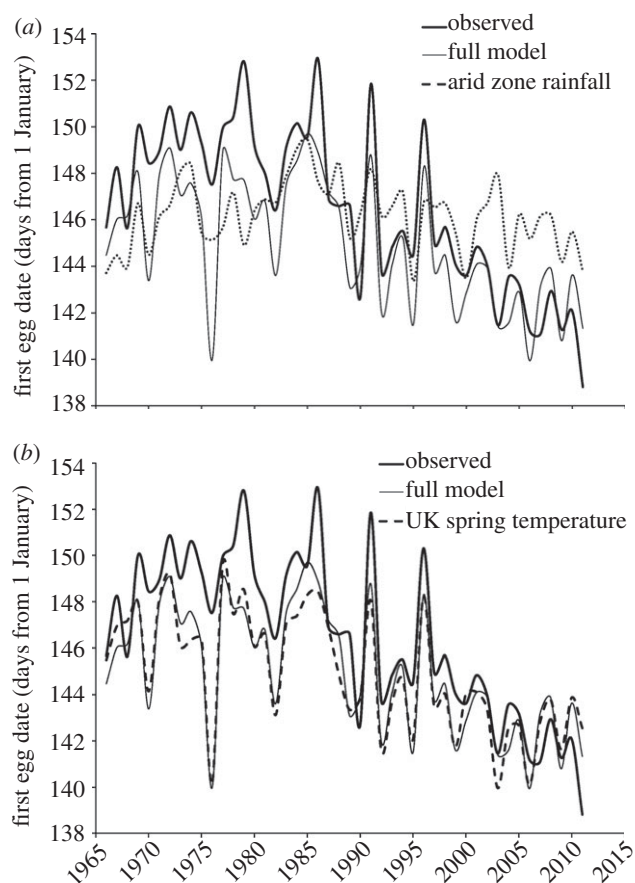
Precipitation on wintering grounds was calculated from dataset TS3.20 [14] as the sum of rainfall from May to October for West Africa (zones (i) and (ii)), and November to March for southern Africa (zone (iii)), the wet-seasons for these regions [15]. Species-specific spring temperature measures were calculated using the Central England Temperature dataset [16], as the mean temperature over the months during which 95% of laying attempts for each species have been recorded across all

years, plus the month prior to this period [17]. Our results were robust to variation in the spring temperature window selected (see electronic supplementary material, appendix S3).

Separate linear mixed models were run for mean annual FED and clutch size using SAS v. 9.2 [18]. Both variables were normally distributed and estimates weighted by the inverse of their standard error, giving less weight to uncertain estimates. Predictor variables were spring temperature on breeding grounds and rainy season precipitation on wintering grounds. Species was included as a random effect, along with interactions between species and climate variables, to ensure that results were generalized across species. The species-specific results can be viewed in the electronic supplementary material, appendix S4. The proportion of variance explained by fixed effects was derived from changes in the variance components of the random effects.

### 3. Results

There was a significant advance in FED through time across all species from 1966 to 2011 ( $F_{1,815} = 287$ ,  $p < 0.001$ ;  $\beta = -0.21$  days/year, 95% CI:  $-0.23, -0.19$ ). Both arid zone precipitation of West Africa and UK spring temperature had significant negative effects on FED across all species (precipitation:  $F_{1,18} = 20.0$ ,  $p < 0.001$ ,  $\beta = -11.0$  days  $m^{-1}$ , 95% CI:  $-15.8, -6.16$ ; temperature:  $F_{1,18} = 120$ ,  $p < 0.001$ ,  $\beta = -3.62$  days/°C, 95% CI:  $-4.27, -2.98$ ). Spring temperature alone explained a much greater proportion of variance in FED (71%) than arid zone precipitation



**Figure 1.** Observed and modelled changes in FED across 19 migrant species between 1966 and 2011. Plots shows predictions from models containing (a) arid zone precipitation or (b) UK spring temperature alone, plus a full model containing both terms that is identical across both panels.

alone (21%; figure 1), accounting for a  $-0.12$  day year $^{-1}$  advance in FED. As the two climate variables were weakly correlated ( $r > 0.26$  between arid zone precipitation and all measures of spring temperature), the addition of arid zone precipitation to the spring temperature model accounted for little additional variance (4%).

There was a significant effect of species' wintering zone on the relationship between arid zone rainfall and FED (wintering zone  $\times$  arid zone rainfall interaction:  $F_{2,778} = 3.43$ ,  $p = 0.03$ ). Species that winter in the arid zone were more negatively affected by arid zone precipitation ( $\beta = -17.0$  days  $m^{-1}$ , 95% CI:  $-24.4, -9.7$ ) than those that winter in the humid zone ( $\beta = -5.9$  days  $m^{-1}$ , 95% CI:  $-11.4, -0.5$ ; contrast:  $F_{1,778} = 5.8$ ,  $p = 0.017$ ). Despite this, spring warming remained the main driver of FED in arid zone species (see electronic supplementary material, appendix S5). FED of the barn swallow *Hirundo rustica*, which winters in the southern zone, was also negatively affected by arid zone precipitation (see electronic supplementary material, appendix S4). Neither humid ( $F_{1,8} = 0.75$ ,  $p > 0.4$ ;  $\beta = -1.34$  days  $m^{-1}$ , 95% CI:  $-4.38, 1.69$ ) nor southern zone ( $F_{1,42} = 0.6$ ,  $p > 0.4$ ;  $\beta = -7.08$  days  $m^{-1}$ , 95% CI:  $-25.1, 10.9$ ) precipitation affected FED of species overwintering in these areas.

Although mean clutch size increased slightly with year ( $F_{1,769} = 3.9$ ,  $p = 0.048$ ;  $\beta = 0.0011$  eggs year $^{-1}$ , 95% CI:  $-0.000011, 0.0021$ ), it was not affected by either arid ( $F_{1,18} = 0.07$ ,  $p > 0.7$ ;  $\beta = -0.032$  eggs  $m^{-1}$ , 95% CI:  $-0.28, 0.21$ ) or humid zone ( $F_{1,8} = 0.3$ ,  $p > 0.6$ ;  $\beta = -0.051$  eggs  $m^{-1}$ , 95% CI:  $-0.24, 0.14$ ) precipitation. Southern zone precipitation negatively affected clutch size in barn swallows ( $F_{1,42} = 6.1$ ,

$p = 0.02$ ,  $\beta = -0.31$  eggs  $m^{-1}$ , 95% CI:  $-0.55, -0.063$ ). Spring temperature in the UK showed a non-significant positive effect on clutch size across all species ( $F_{1,18} = 3.4$ ,  $p = 0.08$ ;  $\beta = 0.033$  eggs  $^{\circ}C^{-1}$ , 95% CI:  $-0.0024, 0.069$ ).

## 4. Discussion

Although precipitation in the arid zone of West Africa was correlated with long-distance migrant laying date, and especially for those migrants that winter in this region, we found little evidence that variation in such conditions had a major influence on FED across all species over 46 years (figure 1a). Breeding ground temperature explained  $3.5\times$  more inter-annual variation in laying date than wintering ground precipitation (figure 1b), and warming accounted for more than half of the observed FED advance [17].

Constraints on the ability of long-distance migrants to adapt to warming on the breeding grounds may increase their vulnerability to climate change [19,20]. Although Sahelian rainfall affects the timing of migrant arrival in Europe [6,7], our result suggests that this is not the main determinant of breeding phenology. Migrants nest earlier in warmer springs, although it remains unclear whether this advance is sufficient to avoid negative population consequences of warming. This adjustment may be achieved through covarying temperature effects on migratory speed across Europe [21]; for example, spring (April–June) temperatures in Spain and England are correlated (1960–2000,  $r = 0.60$ ,  $p < 0.0001$ ). Alternatively, as many migratory species are income breeders [22], using food resources from the breeding grounds for egg production, low temperatures on arrival may limit food availability and delay laying.

Clutch size across all species was weakly correlated with spring temperature and unrelated to African precipitation. This tentatively reinforces the importance of breeding season weather over carry-over effects in determining female breeding decisions. Several hypotheses may account for the lack of carry-over effect on clutch size. Wintering ground precipitation may not affect clutch size if it does not strongly influence arrival phenology. Secondly, after unfavourable winters, individuals may prioritize investment in reproduction over self-maintenance, resulting in carry-over effects on survival [23], which were not examined. Thirdly, any increase in the survival of low-quality females during favourable winters may increase the proportion of small clutches laid, masking any potential carry-over benefit for fitter individuals [24]. Finally, females experiencing favourable climatic conditions may elect to nest earlier rather than lay more eggs.

Humid and southern zone precipitation had little impact on breeding parameters. Arid region savannah vegetation is likely to be most responsive to precipitation, affecting resource availability. The arid zone is also used by the highest number of species and shows the greatest inter-annual fluctuations in precipitation, increasing our analytical power. The apparent negative effect of southern zone precipitation on barn swallow clutch size was an exception; wet winters also reduce survival rates in this species, potentially by reducing foraging conditions [25].

To conclude, we have demonstrated that despite the potential for impacts of climate change on wintering grounds to carry over and affect reproductive decisions [26], when averaged across a range of long-distance migrants the

magnitude of such effects appears small relative to the influence of climate on breeding grounds. However, if future climate change degrades overwintering conditions more than those on breeding grounds, then carry-over effects could become more important through time.

**Data accessibility.** The annual estimates of laying date and clutch size used in this paper can be viewed at <http://www.bto.org/about-birds/birdtrends> and are available from the BTO.

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