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Latitudinal, longitudinal and weather-related variation in breeding parameters of Great Reed Warblers in Europe: A meta-analysis

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Short title Clutch variation in Great Reed Warbler

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Capsule Clutch initiation date decreased with longitude, clutch size increased with latitude and decreased with maximum temperature, whereas the number of fledglings increased both with latitude and longitude, and decreased with maximum temperature in 19 European studies of the Great Reed Warbler. Our study confirmed previous findings about the increasing trend in clutch size with latitude, but also found earlier clutch initiation dates and higher number of fledglings longitudinally from west to east, with precipitation closely associated with clutch initiation date and maximum temperature closely associated with the number of fledglings.

Key words clutch initiation date, clutch size, number of fledglings, geographical gradient, *Acrocephalus arundinaceus*

Clutch size generally decreases with latitude from the poles towards the Equator (Bell 1996, Sanz 1999, Cardillo 2002, Cooper *et al*. 2005, Jetz *et al*. 2008, Griebeler *et al*. 2010, Winkler *et al*. 2014). Griebeler *et al*. (2010) and Jetz *et al*. (2008) explain that this gradient is influenced by seasonality, availability of resources, nest predation, and the length of the breeding season or number of breeding attempts. The longitudinal gradient in clutch size is species specific and is influenced by additional large-scale factors such as the North Atlantic Oscillation index (Sanz 2002) and temperature (Buse *et al*. 1999, Visser & Holleman 2001).

We know much less on large-scale variation in other breeding parameters such as clutch initiation date and number of fledged young (e.g. Carrillo & González-Dávila 2009). Clutch initiation date, which is negatively related to clutch size (Winkler *et al*. 2002), is influenced by temperature and is closely related to the development of vegetation structure (Thyen & Exo 2005, Bourgault *et al*. 2010). The number of fledglings is further strongly influenced by precipitation, predation pressure and availability of resources, most importantly, food during the chick-rearing phase (Dyrcz 1981, Bensch 1993, Fischer 1994, Dyrcz & Flinks 2000, Mérő *et al*. 2014). To understand the variation in breeding success and population dynamics of a species in a wider geographic range, it is thus important to investigate the relationships between breeding parameters, geographical location and environmental factors.

The Great Reed Warbler *Acrocephalus arundinaceus*, a western Palearctic species breeding in reed *Phragmites australis* habitats, is suitable for such investigations because its breeding biology is well described from several locations in Europe (Fig. 1). Latitudinal gradient found in avian clutch size (Jetz *et al*. 2008, Griebeler *et al*. 2010) generally suggests that clutch size of Great Reed Warblers may increase with latitude. However, Dyrcz (1995) found no such trend in his review and variables such as food resources were assumed to determine variation in clutch size. With respect to other breeding parameters, a number of local studies reported that the clutch initiation date and the number of fledglings in the Great Reed Warbler were influenced by the physiognomic structure of reedbeds, air temperature, precipitation and predation pressure (Beier 1981, Dyrcz 1981, Bensch 1993, Fischer 1994, Báldi & Batáry 2005, Dyrcz & Halupka 2009, Mérő *et al*. 2014). In a previous review (Dyrcz 1995), clutch initiation date was also found to be delayed towards the north (although this was not tested statistically).

In this study we explore large-scale latitudinal, longitudinal and weather-related variation in breeding parameters of the Great Reed Warbler. Differences between the seasons are sharper in eastern Europe than in the west, just as seasons in the northern regions differ more than they do in the south (Jetz *et al*. 2008). The climate in the breeding seasons in the eastern and southern parts is mainly hot with limited precipitation (humid continental climate, Mediterranean climate), while in the western and northern parts the summer is usually milder with more precipitation (Atlantic climate, humid continental climate, mild humid temperate climate, and boreal climate; www.weatherspark.com). Considering these climatic differences, we hypothesised that clutch initiation date is earlier in the eastern and southern than in the western and northern parts, and that clutch size and the number of fledglings increase both with latitude and longitude. Furthermore, we hypothesised positive correlations between precipitation and clutch size or number of fledglings and negative correlations between temperature and clutch size or the number of fledglings.

To test our hypothesis we have taken data reported on mean clutch initiation date, clutch size and number of fledglings per nest (as response variables) from 19 European study sites (Table S1, Fig. 1). The study sites longitudinally ranged almost 2000 km, from Switzerland (Dyrcz

1981) to the Pskov region in Russia (Fedorov 2000), and latitudinally c. 2100 km, from Sweden (Bensch 1995) to Turkey (Uzun *et al*. 2014). To explore the variation in these variables across Europe, we used the following parameters as potential explanatory variables: longitude, latitude, maximum temperature (mean temperature in July as the hottest month), daily mean precipitation in mm, the number of days with precipitation, and mean precipitation. Each weather variable was calculated for the breeding period (May, June and July). Data on maximum air temperature and precipitation for each study site were taken from www.climatedata.eu and www.weatherspark.com, respectively.

We applied an information theoretic approach (Burnham & Anderson 2002) to identify those combinations of predictor variables that best describe the variation in the three response variables. We used the ’dredge’ function of package ’MuMIn’ in the R statistical environment (R Core Team 2014) to generate a set of models with combinations of terms of the global model that contained each of the six predictor variables (latitude and longitude along with four weather variables). We then used Akaike’s Information Criterion with correction for finite sample sizes (AICc) to rank models based on their quality (goodness-of-fit vs. model complexity) as recommended in Burnham & Anderson (2002). Finally, to estimate parameters to evaluate the directionality of effects, we calculated model-averaged parameter estimates for regression coefficients and their standard error using the ’model.avg’ function of the MuMIn package.

The results of the analyses showed that the best one-term model for mean clutch initiation date contained the term Longitude, whereas four of the five best two-term models also included Longitude (Table 1). Standardized, model-averaged parameter estimates showed a negative relationship between Longitude and mean clutch initiation date (Table 2), indicating earlier clutch initiation in more eastern localities (Fig. 2), although a simple linear regression did not confirm statistical significance ($F_{1,18} = 1.6$, $p = 0.22$). Variables related to precipitation were frequent in both one-term and two-term models (Table 1), indicating a close relationship between precipitation and clutch initiation date.

The two best one-term models for mean clutch size were either with Maximum Temperature or Latitude, and these variables were part of a number of two-term models for mean clutch size (Table 1). The effect of Latitude was positive (Table 2), indicating increasing clutch size for more northern localities (Fig. 3a, linear regression, $F_{1,18} = 10.8$, $p < 0.01$), whereas the effect of Maximum Temperature was negative, indicating smaller clutches in localities with higher maximum temperatures in the hottest month (Fig. 3b, linear regression, $F_{1,18} = 11.4$, $p < 0.01$).

The best models for mean number of fledglings included one-term models with Maximum Temperature or Latitude and two-term models with Maximum Temperature and either Longitude or Latitude (Table 1). Again, the effects of Latitude and Longitude were positive (Table 2), indicating more fledglings at more northern and eastern localities, whereas that of Maximum Temperature was negative, indicating fewer fledglings in localities with higher maximum temperatures in the hottest month (Fig. 4, linear regression, $F_{1,15} = 8.9$, $p < 0.01$). Maximum Temperature was frequent in the best models (appearing in 9 of 10 best models, Table 1), indicating a close relationship between temperature and number of fledglings.

Our results suggest that in addition to the latitudinal gradient in clutch size, other breeding parameters such as clutch initiation date and number of fledglings can vary longitudinally as well. The lack of a significant simple linear regression between longitude and clutch initiation date suggested that the longitudinal variation could be related to other factors such as temperature and precipitation. Clutch initiation of the Great Reed Warbler was found to depend on the stage of vegetation development which in turn generally depends on precipitation (Dyrcz & Halupka 2009). In addition, clutch initiation date also depends on the age or body size of the adult birds; older and larger adults typically lay eggs and raise young earlier (Summers & Underhill 1991, Claassen *et al*. 2014), which is related to the fact that most of the older birds arrive earlier at their breeding sites (Mérő *et al*. In Press). Finally, clutch initiation date may be delayed independently of arrival, temperature or body size when reedbeds are burnt or mown by humans (Beier 1981, Mérő & Žuljević 2009, Mérő *et al*. 2014). Variation in these factors might be a reasonable explanation for the non-significant trend, because these may vary independently from geographic position, i.e., longitude.

The positive effect of latitude on clutch size in the Great Reed Warbler confirmed the general trend found in various bird species (Jetz *et al*. 2008). The classic explanation for this trend is that clutch size is primarily affected by the abundance of resources in the breeding habitats (Ashmole 1963). The increase of seasonality from the tropics towards the poles, the decrease of nest predation rate and the shortening of the breeding season have also been shown to generate such latitudinal variation in clutch size (Griebeler *et al*. 2010). In a re-evaluation of Ashmole's (1963) hypothesis, Griebeler *et al*. (2004) recognized that besides the seasonality of resources, the cost of reproduction as a second factor was also responsible for the latitudinal gradient in clutch size. In addition, this trend can also be a consequence of factors that limit populations in the non-reproductive period rather than the resources in the breeding period. For example, winter evapotranspiration, which is proportional to primary production, is inversely related to clutch size (Ricklefs 1980). With regard to these more recent explanations, it appears plausible that clutch size of the Great Reed Warbler may depend to some degree on the abundance of resources in the wintering range (Africa) and on the costs of reproduction from the previous breeding seasons. The two best models for clutch size (Table 1) confirm the close association between temperature and latitude, indicating the importance of temperature seasonality. For instance, clutches are smallest in aseasonal environments and increase with temperature seasonality (Jetz *et al*. 2008). In light of these considerations, it is not surprising that clutches of the Great Reed Warbler are larger in more northern regions, where the temperature between the seasons differs considerably, than in more southern regions, where these show smaller variations, respectively.

Our finding that the number of fledglings increased with longitude (and latitude) and decreases with maximum temperature is interesting for several reasons. The number of fledglings is expected to be strongly related to clutch size and affected by resource availability in the chick-rearing period. Although the nestling loss rate is higher than the loss rate of eggs in the Great Reed Warbler (Dyrcz 1981, Petro *et al*. 1998, Batáry & Báldi 2005, Mérő *et al*. 2014), the similar, positive, effect of latitude on clutch size and the number of fledglings found here was as expected. The longitudinal variation, however, may be related to resource availability in the chick-rearing period, which is in turn affected by temperature and precipitation. The abundance of insects, for example, the major food of Great Reed Warblers (Dyrcz & Flinks 2000), depends on temperature and precipitation; less precipitation and higher temperatures result in declining insect abundance and species richness (Frampton *et al*. 2000, Zhu *et al*. 2014). However, based on field studies, it is not clear whether temperature alone influences the gradient in the number of fledglings. In a long-term study by Dyrcz & Halupka (2009), mean temperature in the breeding season did not influence the number of fledglings, whereas in another long-term study by Schaefer *et al*. (2006), the number of fledglings increased with temperature. In addition, the number of fledglings in the Great Reed

Warbler is also influenced by predation rate and brood parasitism by the Common Cuckoo (*Cuculus canorus*) (Moskát & Honza 2000, Mérő et al. 2013). Therefore, we suggest that the decrease in the number of fledglings to the east may depend on a combination of factors such as the temperature-driven availability of insects and the rate of predation and cuckoo parasitism.

In conclusion, we found that clutch initiation date was earlier in more eastern sites and that its variation was probably mostly related to precipitation. Clutch size increased towards the north as expected and was associated negatively with maximum temperature, whereas the number of fledglings increased to the north and to the east as well, and was also negatively associated with maximum temperature. The novelty of these patterns is that they show that breeding parameters can vary longitudinally in addition to the well-known latitudinal variation. A complete explanation of these patterns would require more precise measurements of weather parameters and knowledge on additional factors such as the age structure of breeding populations, predation pressure and parasitism rate at each site, and management of reed beds, all of which probably vary independently from geographical location.

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SUPPLEMENTAL DATA

Additional Supplemental Data can be found in the online version of this article:

Supplemental Data Methods: Table S1

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Table 1. Results of model selection for mean clutch initiation date, clutch size and number of fledged young. LAT - latitude, LONG - longitude, MAXTEMP - mean temperature of the hottest month, MMDAY - daily mean precipitation in mm, MNPREC - mean precipitation in mm, DAYSPREC - number of days with precipitation; all precipitation variables for the breeding period only (May-July). The twelve best models are shown, ranked by model fit based on AICc scores for each response variable.

Response variable	**Rank**	**Model**	**df**	**logLik**	**AICc**	**Δ_{AICc}**	**Weight**
Mean clutch initiation date	1	Intercept only	2	-69.15	143.00	0.00	0.218
	2	LONG	3	-68.51	144.52	1.52	0.102
	3	MMDAY	3	-68.79	145.08	2.08	0.077
	4	MNPREC	3	-69.04	145.57	2.57	0.060
	5	LAT	3	-69.07	145.64	2.64	0.058
	6	MAXTEMP	3	-69.13	145.75	2.75	0.055
	7	DAYSPREC	3	-69.15	145.79	2.79	0.054
	8	MMDAY+MNPREC	5	-66.41	147.10	4.10	0.028
	9	LONG+MMDAY	4	-68.33	147.33	4.33	0.025
	10	LONG+DAYSPREC	4	-68.46	147.59	4.59	0.022
	11	LONG+MAXTEMP	4	-68.47	147.60	4.60	0.022
	12	LONG+LAT	4	-68.48	147.62	4.62	0.022
Mean clutch size	1	MAXTEMP	3	1.26	4.98	0.00	0.187
	2	LAT	3	1.04	5.42	0.44	0.150
	3	LAT+MNPREC	4	1.94	6.78	1.80	0.076
	4	LAT+DAYSPREC	4	1.66	7.34	2.36	0.057
	5	LAT+MAXTEMP	4	1.61	7.45	2.47	0.054
	6	LONG+MAXTEMP	4	1.54	7.59	2.61	0.051
	7	MAXTEMP+MNPREC	4	1.45	7.78	2.80	0.046
	8	MAXTEMP+DAYSPREC	4	1.44	7.78	2.80	0.046
	9	MAXTEMP+MMDAY	4	1.29	8.09	3.11	0.039
	10	LAT+MMDAY	4	1.19	8.29	3.31	0.036
	11	LAT+LONG	4	1.10	8.47	3.49	0.033
	12	LAT+MAXTEMP+MNPREC	5	2.14	10.01	5.03	0.015
Mean number of fledged young	1	MAXTEMP	3	-15.07	37.98	0.00	0.214
	2	LONG+MAXTEMP	4	-13.52	38.36	0.39	0.177
	3	LAT	3	-15.75	39.35	1.38	0.108
	4	LAT+MAXTEMP	4	-14.89	41.11	3.14	0.045
	5	MAXTEMP+DAYSPREC	4	-14.90	41.13	3.15	0.044
	6	LONG+LAT+MAXTEMP	5	-12.96	41.37	3.39	0.039
	7	MAXTEMP+MNPREC	4	-15.05	41.44	3.46	0.038
	8	MAXTEMP+MMDAY	4	-15.05	41.44	3.47	0.038
	9	LONG+MAXTEMP+MMDAY	5	-13.39	42.23	4.26	0.026
	10	LONG+MAXTEMP+MNPREC	5	-13.42	42.28	4.31	0.025
	11	LAT+MNPREC	4	-15.52	42.38	4.40	0.024
	12	LONG+MAXTEMP+DAYSPREC	5	-13.51	42.48	4.50	0.023

Table 2. Standardized, model-averaged parameter estimates for the three response variables.

Response variable	Parameter	Coefficient	S.E.
Mean clutch initiation date	LONG	-0.25	0.25
	MMDAY	0.65	1.21
	MNPREC	-0.59	1.54
	LAT	0.14	0.33
	MAXTEMP	0.03	0.37
	DAYSPREC	0.48	1.16
Mean clutch size	MAXTEMP	-0.57	0.28
	LAT	0.55	0.28
	MNPREC	0.21	0.33
	DAYSPREC	0.16	0.30
	LONG	0.08	0.23
	MMDAY	0.02	0.35
Mean number of fledged young	MAXTEMP	-0.66	0.29
	LONG	0.33	0.25
	LAT	0.35	0.50
	DAYSPREC	-0.11	0.59
	MNPREC	0.15	0.71
	MMDAY	-0.04	0.66

Figure 1. Distribution of the Great Reed Warbler study sites in Europe. Numbers refer to studies listed in Table S1.

Figure 2. Mean clutch initiation date as a function of longitude. Julian date is given as the number of days after April 1.

Figure 3. Mean clutch size as a function of latitude (a) and maximum temperature (b).

Figure 4. Mean number of fledged young as a function of maximum temperature.

Figure 1.

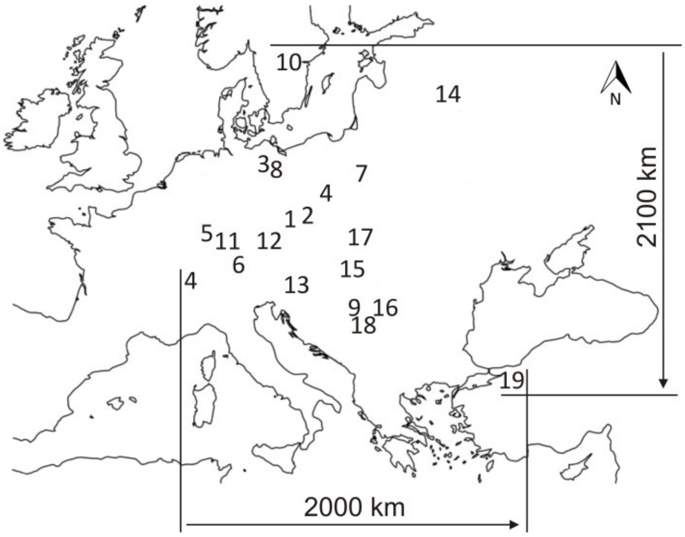


Figure 2.

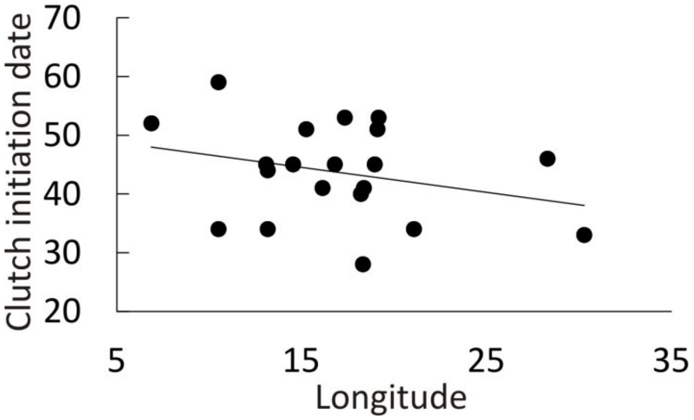


Figure 3.

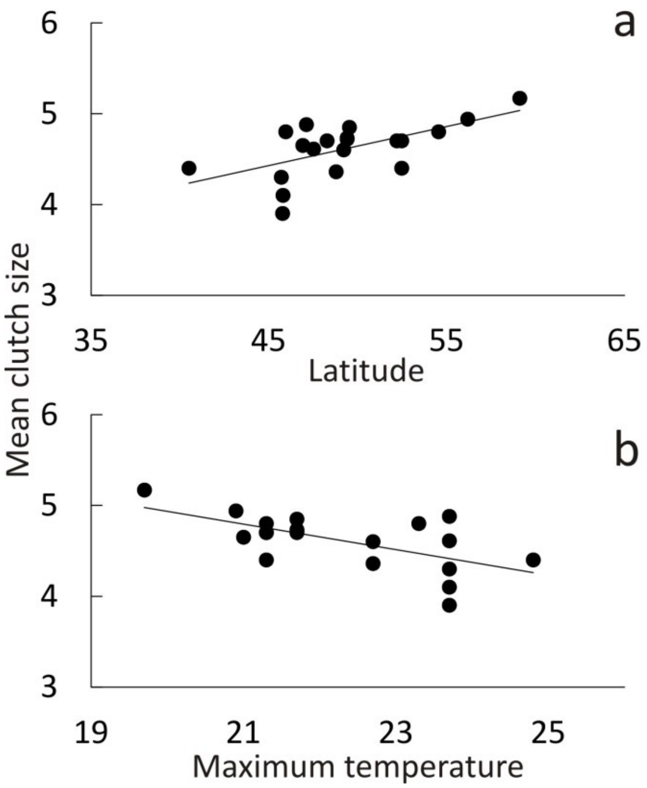
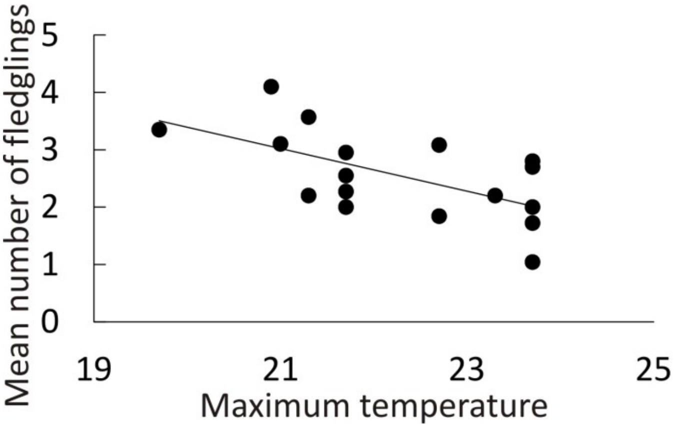

a
b
Mean clutch size
6
5
4
3
35
45
55
65
Latitude
6
5
4
3
19
21
23
25
Maximum temperature

Figure 4.


Mean number of fledglings
0
1
2
3
4
5
19
21
23
25
Maximum temperature