



Geographical variation in reproductive investment across avian assemblages in Europe: effects of environmental drivers differ between altricial and precocial species

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Reproductive traits provide information about the ways by which available resources are allocated during breeding. We tested for environmental drivers of large scale geographical patterns in assemblage mean clutch size, number of broods and overall reproductive investment per breeding season in European birds. We combined data about geographical distribution with published information about reproductive traits, and calculated mean trait values for avian assemblages occurring in 50×50 km grid cells. In total, we employed data from 499 species and 2059 assemblages. As the time available for breeding and the amount of food limit the reproductive effort, we related the geographical variation in reproductive traits to the length of breeding season, normalized difference vegetation index (NDVI) as a surrogate of resource availability, and its seasonality. Geographical patterns in traits may differ between reproductive modes, thus we performed the analyses separately for altricial Passerines ($n = 203$) and precocial non-passerine species ($n = 164$) and controlled for the effect of taxonomy. Large clutches dominated in areas with high NDVI and, in precocial birds, also in areas with high annual seasonality and a long breeding season. High number of broods and high overall reproductive investment dominated in areas with a long breeding season, and high number of broods was found also in areas with low annual seasonality, but only in precocial species. High overall reproductive investment dominated in highly productive areas and also in areas with low annual seasonality in both groups. The increase in reproductive investment is caused mostly by an increase in the number of broods related to the length of season and partly by increase in clutch size related to NDVI. We found a negative correlation between clutch size and the number of broods in Passerines, which might suggest a trade-off between these traits. Processes behind trait patterns differ between altricial and precocial species.

Variation in life histories has attracted considerable scientific attention. In birds, the highly diverse breeding strategies and the traits related to reproductive investment have been a focus of researchers for a long time (Lack 1947, Cody 1966, Ricklefs 1980, Martin 1995, Jetz et al. 2008). In spite of such efforts, we are still missing a complete insight into the processes responsible for the variation in these traits over large spatial scales.

Variation in single avian reproductive investment – often estimated by clutch size – is frequently attributed to the availability of food to birds during breeding. The idea of food limitation was proposed originally by David Lack (1947) who claimed that the number of eggs in a clutch is primarily limited by the amount of food, which parents can provide to their young. Lack's view was further developed by Ashmole (1963) who included the importance of population density. Ashmole (1963) suggested that clutch size depends on the difference between maximum and minimum amount of food available to birds in the course of the year.

During periods when food is scarce (i.e. during winter time in temperate areas) bird populations are kept at relatively low levels. Therefore, an increase in food availability during the breeding season results in higher amount of food available per capita for clutch formation. Consequently, the difference between maximum and minimum food availability across the year (food seasonality) should be positively related to clutch size in birds (Ashmole 1963, Ricklefs 1980, Hořák et al. 2011, 2015).

The most striking spatial difference in clutch size can be observed between tropical and temperate regions, as demonstrated by Jetz et al. (2008) at the global scale. Food limitation is frequently discussed in this context. Smaller clutches could have evolved as a response to relatively lower amounts of food available per capita for breeding in tropical areas (Martin 1996) and/or less time for food collection because of shorter days in the regions close to the equator (Lack 1948). Another hypothesis suggests that stable environment in the tropics generally leads to longer breeding seasons, which

might decrease the investment per one reproductive attempt in favour of increasing the number of reproductive attempts per season (Martin 1995). Although environmental variation is relatively less pronounced across Europe than between temperate and tropical areas, differences in the amount of food, seasonality and season length between northern and southern parts of the European continent might still represent crucial determinants of reproductive allocations in birds (Böhning-Gaese et al. 2000). Moreover, life history theory suggests that clutch size is closely linked to the number of broods during the breeding season. It is generally believed that there is a trade-off between these two traits as energy allocation during reproduction is limited by the total amount of resources available to an individual (Martin 1995). However, the relationship between clutch size and number of broods is not well known (but see Martin 1996, Böhning-Gaese et al. 2000, Griebeler et al. 2010), mostly because the information on the number of broods is difficult to obtain. Anyway, similarly as for the clutch size, several environmental factors have been suggested to determine the number of broods. For instance, the number of broods is directly related to the length of the breeding season (Ricklefs 1966, Stearns 1976, Martin 1996), in accord with a theoretical model (Griebeler et al. 2010). The length of the breeding season is to some extent determined by environmental seasonality (Griebeler et al. 2010). In less seasonal environments, the breeding season is usually longer and thus it might be favourable for birds to spread the risk of nest loss, e.g. due to predation or bad weather (Skutch 1985), over more broods. Conversely, in more seasonal environments it might be advantageous to invest all available energy into one breeding attempt during a period of favourable conditions (Cody 1966, Griebeler et al. 2010). The trends in energetic allocations at large spatial scales are poorly explored, but these are crucial for understanding environmental drivers of reproductive investment. Some studies have focused on single species (Yom-Tov 1987, König and Gwinner 1995), but the relationship between the number of clutches per breeding season and season length or the degree of seasonality across multiple species has not been examined so far over large spatial scales. Finally, gradients in food resources may affect the overall reproductive investment or the allocation between clutch size and the number of broods (Bennett and Owens 2002, Robinson et al. 2010). As far as we know, no study has dealt with this issue by employing large datasets concerning whole avian assemblages, i.e. focusing on all breeding species in particular areas. By looking at spatial patterns of the overall reproductive investment per season (estimated using the combination of information about clutch size, egg size and number of broods), we can test whether smaller clutches are compensated by a higher number of broods, and in addition, whether changes in the total reproductive investment can be attributed to the variation in clutch size or the number of broods.

In this study, we focus on European birds as their life history traits are well described and reliable data about their breeding distributions are available. Our general goal is to explore how environmental conditions affect large-scale spatial variation in assemblage means of fundamental reproductive traits. In particular, we focus on the following objectives. First, we aim to describe the continental-scale variation in clutch size, number of broods and overall

reproductive investment (here estimated as clutch size \times egg mass \times number of broods) per breeding season. Second, we test whether environmental parameters representing food availability, its annual seasonality (i.e. the temporal variation in food availability throughout the year) and length of the breeding season affect spatial variation in reproductive investment. Specifically, we predict that: 1) clutch size increases with increasing food availability during the breeding season as well as with its annual seasonality, as it increases per capita food availability during the breeding season (Ashmole 1963). Furthermore, we predict that clutch size decreases with increasing length of the breeding season because more time available for breeding should lower investment per reproductive attempt in favour of having more reproductive attempts (Martin 1995); 2) The number of broods per season increases with increasing length of the breeding season but decreases with increasing seasonality as it is strongly linked to time available for reproduction; in more seasonal environments the 'time window' suitable for breeding might be shorter. Moreover, we suggest that food availability during breeding season has no effect on the number of broods when remaining environmental variables (i.e. annual seasonality and the length of the breeding season) are controlled for, as food availability positively influences the investment into a single reproductive event (clutch size); 3) Overall reproductive investment should be positively influenced by both food availability during breeding (as it increases single reproductive investment) and the length of the breeding season (as it allows more breeding attempts). In relation to the previous predictions that fewer larger clutches are expected in more seasonal environments, overall reproductive investment is expected to be lower at such locations because birds are not able to compensate fully for the lower number of broods by increased clutch size due to parental feeding limitations. Finally, we aim to test the expected negative correlation between clutch size and the number of broods per season across a large spatial scale. We will analyse altricial and precocial birds separately because we assume that the differences in their reproductive mode (such as absence of parental feeding in precocial species) could be reflected in different spatial patterns in reproductive traits and their different relations to environmental factors.

Materials and Methods

Avian traits and breeding distribution

We compiled information about egg mass, clutch size and number of broods per breeding season (replacement broods were not included) for all 499 European bird species from the interactive version of the Birds of the Western Palearctic handbook (Cramp 2006). We are aware of the fact that trait values vary across geographical ranges of individual species (José Sanz 1996, Encabo et al. 2002). However, inter-specific variation is in most cases higher than intra-specific one, with the exception of some passerines, whose southern populations are documented to lay half as many eggs as the northern populations (Dunn et al. 2000). Since comprehensive information about intra-specific geographical

variation in traits is not available at the scale of our study, we used mean trait values, calculated from the available range of population values. This approach has been frequently used in previous studies (Greve et al. 2008, Jetz et al. 2008, Olson et al. 2009, Hořák et al. 2015) and we assume that it is able to capture strongly pronounced and biologically relevant patterns over large scales. Note that intra-specific variation in the direction as described above would even strengthen the patterns revealed using mean trait values. We excluded two species of brood parasites (*Cuculus canorus* and *Clamator glandarius*) from the dataset as they have a considerably different mode of reproduction.

We also computed an aggregated breeding trait for each bird species called 'overall reproductive investment'. Reproductive investment during one breeding attempt is usually calculated as clutch size \times egg mass (Delhey et al. 2010, Robinson et al. 2010). As we have been interested in reproductive investment for the whole breeding season, we used the number of broods per breeding season and calculated overall reproductive investment as clutch size \times egg mass \times number of broods per breeding season. Since egg mass is highly correlated with female body mass (Rahn et al. 1975) (Pearson's correlation coefficient = 0.97, $p < 0.001$, in our data), we additionally compiled the information about female body mass (Cramp 2006) and made a linear regression of egg mass on female body mass (both \log_{10} -transformed to achieve normality of data). We then used residuals from that regression instead of raw egg mass values to reveal the relative egg mass investment. Thus, we used the residuals of egg mass along with the size of clutch and the number of broods to calculate the overall reproductive investment.

We combined the information about bird traits with data about species' breeding distribution obtained from the European Bird Census Council (EBCC) Atlas (Hagemeijer and Blair 1997). Presence/absence information was available for 3952 grid cells whose size was 50×50 km. From available grid cells we used only those which fulfilled the following criteria: 1) occurrence of more than 10 breeding species, 2) more than 50% of a grid cell total area composed of land, 3) species coverage classified as 'good' according to EBCC criteria, meaning that at least 75% of expected breeding species were recorded according to the experience of researchers with knowledge of the given area. We excluded Iceland from the analyses as it is biogeographically remote from the continental Europe, and island effects together with extreme climatic conditions presumably play a key role in structuring local assemblages (Wiens and Donoghue 2004). Inclusion of such a region in the models could eventually shift geographical trends and obscure their interpretations. Therefore, we used 2059 map grid cells in total for the analyses. We consider each grid cell as a local avian assemblage.

Environmental variables

To test the abovementioned hypotheses, we used three environmental variables in our models. First, the length of the breeding season (hereafter 'length of season') was defined as the period when birds lay eggs. To estimate the length of the breeding season for each grid cell, we took the information about the beginning and the end of the breeding period for each bird species from Cramp (2006). Then we calculated

mean values of the beginning and the end of the season for all bird species occurring in a given grid cell, thus obtaining assemblage mean of season length for all grid cells in Europe. In addition, we used an alternative estimate of the length of breeding season. Assuming that breeding birds depend mainly on insects that depend on vegetation, we measured the length of breeding season by the vegetation growth period. We used the growing degree day (GDD) information, which is based on the mean daily temperature suitable for growing of vegetation; the information was obtained from climate research unit (www.cru.uea.ac.uk). We computed the number of GDDs in particular grid cells which gave us the information about season length (more GDDs means longer growing season). The analyses revealed that both metrics of breeding season length provided similar results, thus we decided to use the first one based on breeding period information (results for GDD are provided in the Supplementary material Appendix 2 Tables A3–A5).

Second, the estimates of environmental productivity were based on remote sensing data concerning the Normalized Difference Vegetation Index (hereafter 'NDVI') obtained from the global land cover facility (www.landcover.org), which contains information about monthly value of NDVI for the period 1982–2006 (Pinzon et al. 2005, Tucker et al. 2007). Specifically, we used the sum of NDVI values during the breeding season (hereafter 'sum of NDVIbreed') as the surrogate of the overall level of resources during the breeding season. Third, to estimate the annual seasonality in food resources we used the difference between maximum and minimum NDVI over the course of a year (hereafter 'seasonality in NDVIyear'). As NDVI describes 'greenness' of vegetation and has been shown to be closely correlated with rainfall, total green biomass and net primary productivity (Chong et al. 1993, Schmidt and Karnieli 2002), we assume that its variation reflects the differences in the amount of food available to birds over large spatial scales, although we admit that large scale estimates of environmental productivity are only rough proxies for real food availability to birds. Still, the amount of food for breeding, such as arthropod abundance, correlates with overall plant productivity and biomass (Gordo 2007), and there is also direct evidence for a positive relationship between arthropod abundance and NDVI (Lafage et al. 2013). We adjusted raw data on abovementioned environmental variables for grid cell size used in this study (i.e. grids 50×50 km) and calculated mean values in ESRI ArcGIS 9.2 (<http://www.esri.com>). We excluded data from years 1994 and 2000 as they have been reported to be abnormal (Tucker et al. 2007). We found correlations between the following environmental variables: sum of NDVIbreed and length of season (Pearson's correlation coefficient $r = 0.48$), sum of NDVIbreed and seasonality in NDVIyear (Pearson's correlation coefficient $r = -0.1$), and seasonality in NDVIyear and length of season (Pearson's correlation coefficient $r = -0.58$). However, all these values are small enough to include all environmental variables as non-independent into a single statistical model (Dormann et al. 2013).

Geographical patterns in reproductive traits

In order to describe the geographical patterns of avian reproductive traits we calculated the assemblage mean trait

values for each local avian assemblage (each grid cell). As reproductive strategies of birds are very diverse and this variation might reflect the ways by which birds allocate available energy into reproduction, we performed the analyses separately for precocial species ($n = 164$) and Passerines representing altricial species ($n = 203$). We also did the analyses for all bird species together ($n = 499$, Supplementary material Appendix 1). We considered members of following families as precocial: Gaviidae, Podicipedidae, Phoenicopteridae, Anatidae, Tetraonidae, Phasianidae, Turnicidae, Rallidae, Gruidae, Otidae, Haematopodidae, Recurvirostridae, Burhinidae, Glareolidae, Charadriidae, Scolopacidae, Laridae, Sternidae and Pteroclididae. Altricial species were represented by Passerines, even though altricial species can be also found among non-passerines. In order to deal with phylogenetic non-independence we controlled for avian taxonomy in the analyses. For each trait we did the one-way Anova analysis with taxonomical family as a factor and the value of a trait as the dependent variable, which is a commonly used method (Brawn et al. 1995, Nabholz et al. 2009). We used taxonomical classification based on phylogeny of Jetz et al. (2012) and chose family level rather than genus level, because genera usually do not include sufficient number of species (many of them are even monospecific). We then used residual values corrected for family membership in further calculations. To achieve normality of data, we \log_{10} -transformed all breeding trait data (Bera et al. 1984).

In a first step, we tested for the relationships between assemblage means of reproductive traits (clutch size, number of broods per season, reproductive investment per season) and three geographical variables – latitude, longitude and altitude. Second, we investigated relationships between assemblage means of reproductive traits and three environmental variables (seasonality in NDVI_{year}, sum of NDVI_{breed} and length of season). As our data indicated a high spatial autocorrelation, i.e. the neighbouring locations were more similar than would be expected by chance (Legendre 1993), we decided to control for the spatial non-independence by employing the Generalized Least Squares regression model with a fitted semi-variogram (hereafter GLS, Rangel et al. 2006) rather than using simply Ordinary Least Squares regression models (White 1980). We processed the GLS models also with assemblage mean of traits after controlling for taxonomy (hereafter 'GLS_{tax}'). When interpreting the results, we favoured the variables whose importance was comparable in both GLS and GLS_{tax} models as we believe that similar results given by the two different models indicate that the relationship is not driven by phylogenetic non-independence. In addition, we tested for the relationship between assemblage mean clutch size and the number of broods per season using correlation coefficient controlled for spatial autocorrelation according to Dutilleul et al. (1993). Dutilleul's modified t-test uses Moran's I estimates of spatial autocorrelation in the data, correcting the degrees of freedom and adjusting sample size to test the significance of the correlation. We performed models with all possible combinations of explanatory environmental variables and chose the best model according to the minimal value of Akaike Information Criterion (AIC, Diniz-Filho et al. 2008). We estimated the importance of independent variables using the Standardized Coefficient (hereafter 'std coeff') which ranges

from +1 to -1, so that the closer the value of std coeff of the independent variable is to +1 or -1, the larger is its positive or negative, respectively, influence on the dependent variable (Kissling et al. 2008, Bini et al. 2009).

To test statistically the differences in spatial patterns of traits between altricial and precocial species, we performed analyses containing pooled data for both groups and tested the interactions between geographical (latitude, longitude and altitude) and environmental (the sum of NDVI_{breed}, seasonality in NDVI_{year} and the length of the breeding season) variables and reproduction mode (altricial/precocial, hereafter 'young') on reproductive traits (clutch size, the number of broods per season and reproductive investment per season). These models tested only the difference between altricial and precocial species and not if the effect of the interaction between altricial/precocial species and explanatory variables on the reproductive traits is positive or negative. We provided results of these analyses in the Supplementary material Appendix 3 Table A6, A7.

We ran the statistical models in R (R Core Team) using packages 'stats' and 'nlme', and we used SAM 4.0 (Rangel et al. 2010) for the visualization of spatial patterns.

Results

Geographical patterns in traits

Assemblage means of avian reproductive traits showed pronounced geographical patterns across Europe. In altricial birds, assemblage mean clutch size increased significantly with increasing latitude (Table 1) and there was also a relatively weaker but statistically significant negative relationship with longitude. Overall, species with the largest clutches dominated in the central parts of Europe (Fig. 1a). Although all geographical correlates were significant also in precocial species (Table 1), their geographic patterns in clutch size appeared weaker compared to altricial species (Fig. 1b).

Altricial species with the lowest number of broods dominated in northern and eastern regions of Europe (Table 1, Fig. 2a). Surprisingly, there was a positive relationship between altitude and the number of broods, but the effect of altitude was very small compared to the effect of geographical coordinates. Similarly, as in the case of clutch size, the number of broods in precocial species showed a weaker spatial pattern (Fig. 2b) than in altricial species. Still, the decrease of the number of broods both with increasing latitude and longitude was significant.

Altricial species with the highest overall reproductive investment dominated in western Europe (Table 1, Fig. 3a). In contrast, we observed no clear spatial pattern in reproductive investment in precocial species (Fig. 3b).

The relationship between clutch size and number of broods

Clutch size of altricial birds (Fig. 1a) appears to show an inverse spatial pattern to the number of broods per season (Fig. 2a). Therefore, we decided to explicitly test the relationship between clutch size and the number of broods to see if there was a significant negative relationship, which might

Table 1. Geographical correlates of assemblage mean clutch size, the number of broods per season and reproductive investment per season in European birds. Altricial and precocial birds are analyzed separately. Importance of geographical variables is indicated by the values of standardized coefficients.

	Altricial birds		Precocial birds	
	GLS std coeff	SE	GLS std coeff	SE
Clutch size				
Latitude	0.797*	<0.001	-0.32*	0.007
Longitude	-0.262*	<0.001	0.49*	0.004
Altitude	-	-	0.349***	<0.001
F	243.11		65.2	
r ² predict	0.192		0.087	
r ² total	0.804		0.684	
AIC predict	-13648.15		-5148.07	
AIC total	-16556.46		-7414.02	
Number of broods per season				
Latitude	-0.305*	<0.001	-0.373*	<0.001
Longitude	-0.53*	<0.001	-0.196*	<0.001
Altitude	0.042**	<0.001	-	-
F	1266.79		825.41	
r ² predict	0.65		0.447	
r ² total	0.9		0.661	
AIC predict	-12498		-10436.77	
AIC total	-15055.94		-11434.46	
Reproductive investment per season				
Latitude	-	-	-	-
Longitude	-0.675**	<0.001	-	-
Altitude	-	-	-	-
F	3197.08		-	-
r ² predict	0.609		-	-
r ² total	0.802		-	-
AIC predict	-12611.26		-	-
AIC total	-14003.52		-	-

GLS = generalized least squares regression model; std coeff = standardized coefficient; SE = standard error; F = F statistic; r² predict = variability explained by predictor variables; r² total = variability explained by predictor variables and space; AIC predict = Akaike information criterion (AIC) of the model containing only predictor variables; AIC total = AIC of the model containing predictor variables and space; *p < 0.05; **p < 0.01; ***p < 0.001.

suggest an existence of a trade-off over geographical space. In altricial birds, we found a negative and marginally significant correlation between clutch size and number of broods (Pearson's $r = -0.361$, spatially corrected $p = 0.05$, Fig. 4). In contrast, the analysis revealed a positive correlation in precocial species (Pearson's $r = 0.429$, spatially corrected $p = 0.033$).

Environmental determinants of trait variation

Clutch size

In altricial birds, assemblage mean clutch size increased with increasing sum of NDVI_{breed} (Table 2). However, the variation explained solely by the sum of NDVI_{breed} in both the GLS and GLS_{tax} model was very low (r^2 Predict = 5.4 and 0.1 %, respectively), and thus the results have to be considered with caution.

The situation was slightly different in precocial birds, in which assemblage mean clutch size increased with increasing sum of NDVI_{breed} (Table 2) but also with the length of season. The GLS model further supported an increase in clutch size with increasing seasonality in NDVI_{year}.

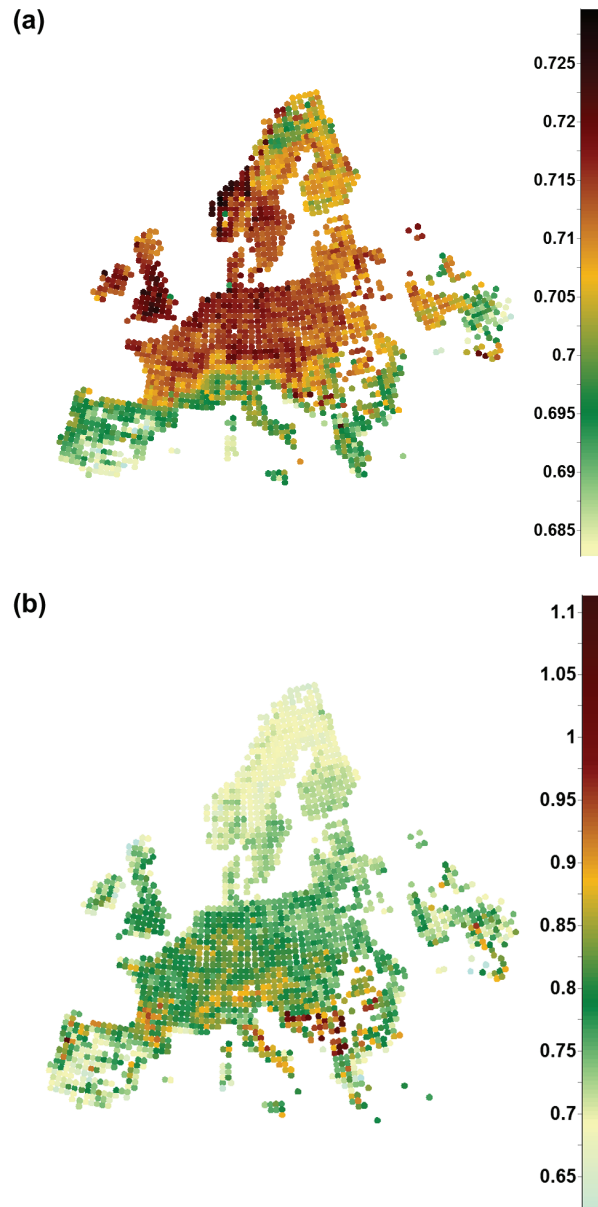


Figure 1. Geographical variation in clutch size. Mean values of clutch size for each local assemblage (grid cell 50×50 km) are visualized for altricial (a) and precocial species (b). The colours refer to \log_{10} transformed values of assemblage means.

In summary, the sum of NDVI_{breed} seems to be the most important variable influencing clutch size in both groups as it was significant in all models (Table 2).

Number of broods per season

In altricial birds, assemblage mean number of broods was positively affected by the length of the season (Table 3) and by sum of NDVI_{breed}. However, the later relationship was relatively weak and was statistically significant only in the GLS_{tax} model.

In precocial birds, we found that the length of the season had the strongest and positive effect on assemblage mean number of broods (Table 3). We also found a weaker negative effect of seasonality in NDVI_{year}.

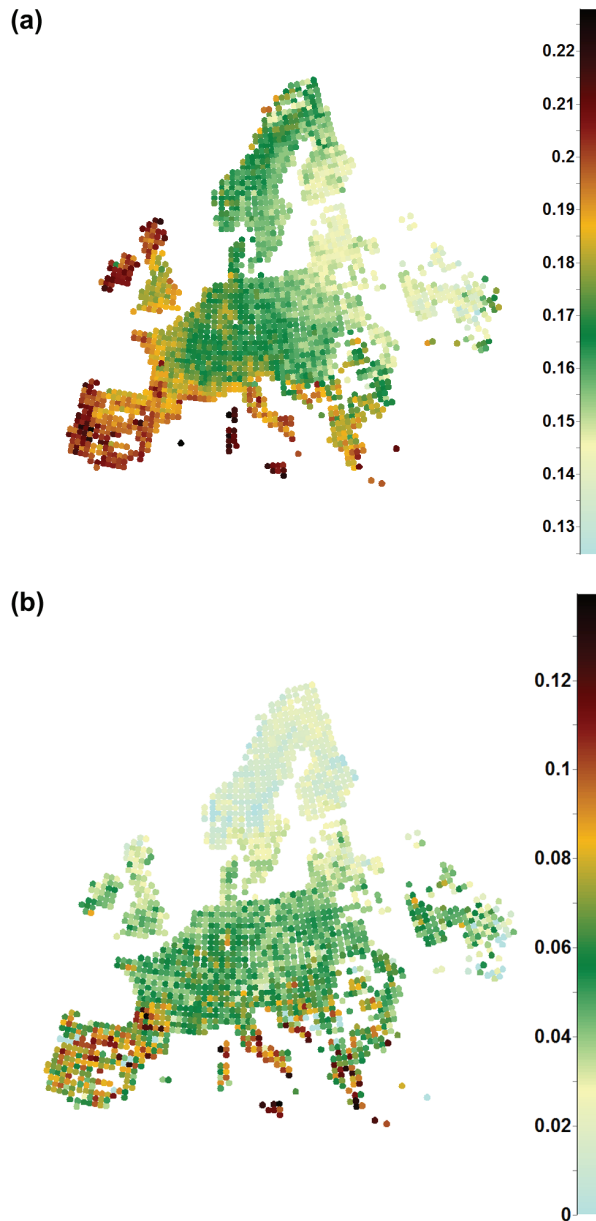


Figure 2. Geographical variation in the number of broods per season. Mean values of number of broods for each local assemblage (grid cell 50×50 km) are visualized for altricial (a) and precocial species (b). The colours refer to \log_{10} transformed values of assemblage means.

In summary, the length of the breeding season appeared to be a crucial factor influencing the number of broods in all models and both avian groups (Table 3).

Overall reproductive investment per season

In altricial birds, assemblage mean reproductive investment was related most strongly and positively to the length of the season (Table 4). We also found a positive effect of sum of NDVI_{breed} but this effect was weaker and significant only in the GLS_{tax} model. Similarly, the negative effect of seasonality in NDVI_{year} was rather weak and was significant only in the GLS model that did not control for taxonomy.

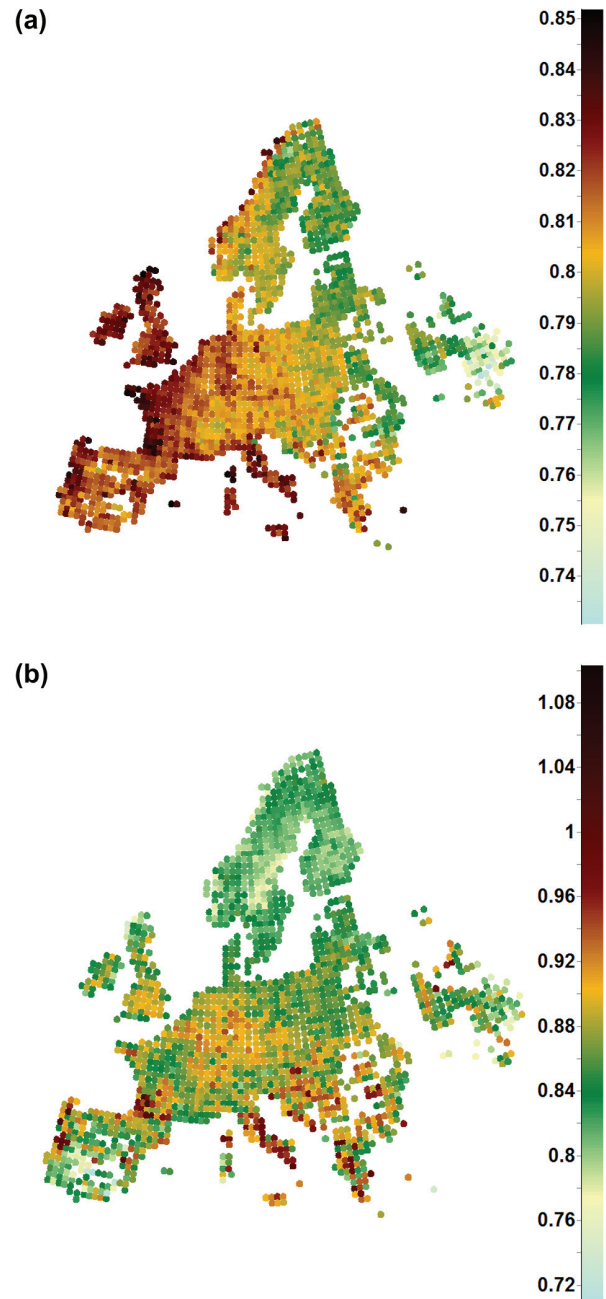


Figure 3. Geographical variation in reproductive investment per season. Mean values of reproductive investment for each local assemblage (grid cell 50×50 km) are visualized for altricial (a) and precocial species (b). Reproductive investment values were calculated as \log_{10} (clutch size \times number of broods per season \times female-mass corrected egg mass). The colours refer to values of assemblage means.

We found a similar situation in precocial birds. Reproductive investment increased with increasing length of the season (Table 4), and also with increasing sum of NDVI_{breed}. Finally, reproductive investment decreased with increasing seasonality in NDVI_{year} in the GLS_{tax} model only.

In summary, the length of the breeding season and the sum of NDVI during the breeding season were the most

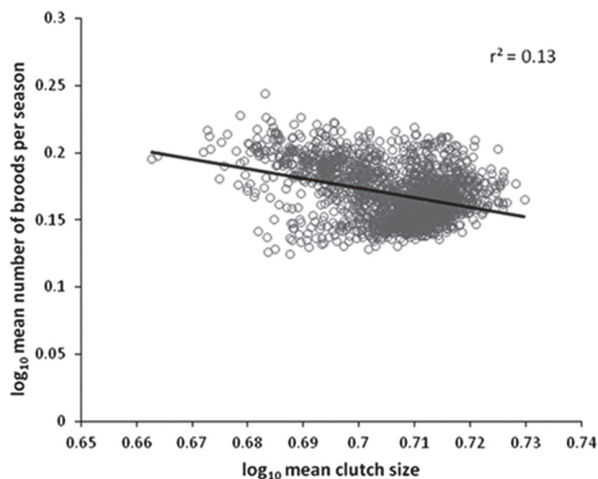


Figure 4. Relationship between mean clutch size and the number of broods per season in altricial birds across the avian assemblages (grid cell 50 × 50 km). Clutch size and the number of broods were \log_{10} transformed before calculation of the means. r^2 , coefficient of determination.

important factors affecting the overall reproductive investment in both altricial and precocial species (Table 4).

Discussion

Geographical patterns in reproductive traits

Our study reveals interesting spatial patterns in reproductive traits across avian assemblages in Europe. Altricial species with large clutches dominate in northern areas, in accord with the global latitudinal pattern of clutch size described by Jetz et al. (2008) who used data at a more coarse-grained resolution. In contrast, precocial species with large clutches dominate rather in the southern parts of Europe and surprisingly also at high altitudes. Larger clutches at higher altitudes reported here seem to be in conflict with patterns described by other studies, which found species with smaller clutches at higher altitudes (Badyaev 1997, typically in the

tropics: Freeman and Mason 2014, Boyce et al. 2015), nevertheless, the studies focused only on altricial Passerines. Although the mechanisms remain unexplored, theoretically, the shorter breeding seasons and generally less stable and less predictable conditions could support species with few larger clutches in temperate zone mountains. However, birds have generally higher reproductive investment in lowlands (Bears et al. 2009), so the predicted elevational trends in clutch size may not be straightforward.

Altricial species with a greater number of broods per season dominate in the south-western areas but this pattern was less pronounced in precocial species. Interestingly, altricial species with the highest reproductive investment were found in the western parts of Europe, although there was no clear pattern in precocial species. These results suggest that the longitudinal gradient of continental climate affects the overall reproductive investment in European birds more strongly than latitude (cf. Böhning-Gaese et al. 2000). Generally, however, the geographical patterns in reproductive traits differed between altricial and precocial species, being relatively clear in the altricial birds but rather weak in the precocial ones (Fig. 1–3 and Supplementary material Appendix 3 Table A6, A7).

In our analyses, we used the assemblage mean values of reproductive traits and we omitted the (unknown) intra-specific variability in particular traits. Therefore, the reported patterns might not reflect the ‘true’ geographical variability in reproductive traits. However, neglecting intra-specific variability can only weaken real geographical trends. In other words, the real geographical patterns in traits, which would include intra-specific variability, are not expected to be entirely different from the patterns we have reported, but may be more pronounced. For instance, we can only presume that the individuals breeding in the northern and middle parts of Europe lay even larger clutches than that species’ mean clutch size. The opposite might hold for birds breeding in southern areas, and the absolute differences between areas might be thus actually considerably larger. Similarly, the number of broods laid by birds breeding in southern and western areas might be even higher than our assemblage means indicate.

Table 2. Environmental correlates of assemblage mean clutch size in European birds. Altricial and precocial birds are analyzed separately. Results for GLS regression models are provided for both raw data and data controlled for taxonomy. Importance of independent environmental variables is indicated by the values of standardized coefficients.

	Altricial birds				Precocial birds			
	GLS std coeff	SE	GLS tax std coeff	SE	GLS std coeff	SE	GLS tax std coeff	SE
Seasonality in NDVI _{year}	–	–	–	–	0.28***	<0.001	–	–
Sum of NDVI _{breed}	0.132***	<0.001	0.042*	<0.001	0.245***	<0.001	0.209***	<0.001
Length of season	–	–	–	–	0.191***	0.021	0.084*	0.004
F	116.80		0.21		146.34		275.30	
r^2 predict	0.054		0.001		0.177		0.212	
r^2 total	0.773		0.779		0.592		0.543	
AIC predict	–13326.93		–15370.08		–5459.33		–12359.16	
AIC total	–16254.40		–18474.8		–6894.95		–13475.80	

GLS = generalized least squares regression model; GLS tax = model with clutch size controlled for taxonomy (see methods); std coeff = standardized coefficient; SE = standard error; NDVI = normalized difference vegetation index; F = F statistic; r^2 predict = variability explained by predictor variables; r^2 total = variability explained by predictor variables and space; AIC predict = Akaike information criterion (AIC) of the model containing only predictor variables; AIC total = AIC of the model containing predictor variables and space; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 3. Environmental correlates of assemblage mean of the number of broods per season in European birds. Altricial and precocial birds are analyzed separately. Results for GLS regression models are provided both for raw data and data controlled for taxonomy. Importance of independent environmental variables is indicated by the values of standardized coefficients.

Number of broods per season	Altricial birds				Precocial birds			
	GLS std coeff	SE	GLS tax std coeff	SE	GLS std coeff	SE	GLS tax std coeff	SE
Seasonality in NDVI/year	–	–	–	–	–0.024	<0.001	–0.075	<0.001
Sum of NDVI/breed	–	–	0.045**	<0.001	–	–	–	–
Length of season	0.268***	0.003	0.297***	0.002	0.206***	0.007	0.101**	0.004
F	716.56		456.36		239.2		151.2	
r ² Predict	0.26		0.31		0.19		0.13	
r ² Total	0.9		0.9		0.687		0.57	
AIC Predict	–10965.74		–12150.61		–9656.04		–11892.1	
AIC Total	–14979.28		–16056.46		–11597.12		–13322.6	

GLS = generalized least squares regression model; GLS tax = model with the number of broods per season controlled for taxonomy (see methods); std coeff = standardized coefficient; SE = standard error; NDVI = normalized difference vegetation index; F = F statistic; r² predict = variability explained by predictor variables; r² total = variability explained by predictor variables and space; AIC predict = Akaike information criterion of the model containing only predictor variables; AIC total = AIC of the model containing predictor variables and space; *p < 0.05; **p < 0.01; ***p < 0.001.

The effects of environmental conditions on reproductive traits

Clutch size of both altricial and precocial species was positively affected by the sum of NDVI during the breeding season, as predicted. However, the results for altricial birds have to be considered with caution as NDVI during breeding explained only small proportion of variation (5.4 %). Also, seasonality in NDVI affected clutch size variation positively, but only in precocial species. The lack of the effect of annual seasonality on clutch size in altricial birds is quite surprising and in contrast to predictions (Ashmole 1963) as well as to findings of previous studies (Ricklefs 1980, Martin 1995, Jetz et al. 2008, Hořák et al. 2011, 2015, Evans et al. 2005, but see Dunn et al. 2000, Rose and Lyon 2013). We can only speculate about the reasons. For instance, migratory birds, which utilize the surplus of spring resources in European communities, may consequently weaken the effect of seasonality on per capita food availability during the breeding season. Surprisingly, we found no effect of the length of the breeding season on clutch size in altricial birds, and even a positive effect in precocial species. We expected

a negative relationship because longer breeding seasons support more clutches (see below) and thus could lower investment per breeding attempt. Our finding might thus indicate that the presumed trade-off between clutch size and number of broods is not so strong and birds are not forced to reduce clutch size in favour of the number of clutches produced in a longer breeding season (but see the discussion below).

The number of broods in both altricial and precocial species was most strongly and positively related to the length of the breeding season. Such a finding supports the assumption that birds can afford more clutches if they have more time for breeding and agrees with theoretical conclusions of Farnsworth and Simons (2001) and Griebeler et al. (2010). In addition, we reported a weak negative effect of annual seasonality on the number of broods in precocial species, which again highlights the importance of the length of ‘temporal window’ with conditions suitable for breeding. However, we found no such pattern in altricial species. It can be related to the fact that within families of Passerines and after controlling for remaining environmental variables, the number of broods was slightly positively influenced by environmental productivity during breeding. This suggests that altricial

Table 4. Environmental correlates of assemblage mean reproductive investment per season in European birds. Altricial and precocial birds are analyzed separately. Results for GLS regression models are provided both for raw data and data controlled for taxonomy. Importance of independent environmental variables is indicated by the values of standardized coefficients.

Reproductive investment per season	Altricial birds				Precocial birds			
	GLS std coeff	SE	GLS tax std coeff	SE	GLS std coeff	SE	GLS tax std coeff	SE
Seasonality in NDVI/year	–0.064*	<0.001	–	–	–	–	–0.159***	<0.001
Sum of NDVI/breed	–	–	0.056**	<0.001	0.196***	<0.001	0.061*	<0.001
Length of season	0.241***	0.004	0.298***	0.003	0.091*	0.014	0.004	0.008
F	458.62		291.86		213.61		91.323	
r ² Predict	0.309		0.222		0.173		0.118	
r ² Total	0.795		0.835		0.495		0.471	
AIC Predict	–11439.84		–12216.48		–7237.56		–10026.92	
AIC Total	–13930.44		–15401.66		–8247.24		–11070.9	

GLS = generalized least squares regression model; GLS tax = model with reproductive investment per season controlled for taxonomy (see methods); std coeff = standardized coefficient; SE = standard error; NDVI = normalized difference vegetation index; F = F statistic; r² predict = variability explained by predictor variables; r² total = variability explained by predictor variables and space; AIC predict = Akaike information criterion of the model containing only predictor variables; AIC total = AIC of the model containing predictor variables and space; *p < 0.05; **p < 0.01; ***p < 0.001.

species might increase the number of reproductive attempts as a response to abundant food resources and are not affected by their seasonality.

Overall reproductive investment was positively related to the sum of NDVI during the breeding season and to the length of the breeding season. The hypothesis of larger reproductive investment in longer breeding season was empirically supported at the intra-specific level for instance by Jacobs et al. (2013), who showed that western bluebirds *Sialia mexicana*, which started to lay eggs early in the season, were more likely double-brooded as they had more time available for reproduction and thus could afford second clutches. Similarly, Ricklefs and Bloom (1977) described a positive relationship between the number of fledglings and the length of the breeding season in 35 American passerines. Our findings support the idea that birds increase their reproductive investment mostly by multiplying reproductive attempts in longer breeding seasons and by larger clutches in more productive environments (Delhey et al. 2010, Jacobs et al. 2013). We also found a weak negative effect of environmental seasonality on overall reproductive investment. Together with the previous results, this finding supports the assumption that the lower overall reproductive investment in more seasonal environments is a consequence of parent's inability to fully compensate for a shorter breeding season (and thus fewer clutches) by larger clutches due to feeding limitations.

The relationship between clutch size and number of broods

We found a marginally negative relationship between clutch size and number of broods per breeding season in altricial species. In contrast, our analyses suggested a positive relationship in precocial species. Altricial species with more broods and smaller clutches are typically found in southern parts of Europe and the opposite holds true in northern regions (Fig. 1a, 2a). Therefore, this pattern could be a result of differential allocation of energy into breeding under varying environmental conditions (namely the length and seasonality of the breeding season). Martin (1995) provided evidence for the trade-off between clutch size and the number of broods in North American Passeriformes and Piciformes. At intra-specific level, Lindén (1988) experimentally manipulated the size of clutches in great tits *Parus major*, and has shown that birds with enlarged first clutches produced less likely the second ones. Although a trade-off between clutch size and number of broods is predicted by life-history theory (Stearns 1976), it has not been documented very often so far, and never at the whole assemblage level. Our results suggest possible trade-off between these life-history traits over large geographical scale. However, we found no such evidence in precocial species.

Precocial versus altricial species

Our analyses revealed marked differences in spatial patterns of assemblage mean trait values between precocial and altricial species (results of statistical tests are available in Supplementary material Appendix 3 Table A6, A7). This can be due to their distinct reproductive strategies (Bennett and Owens 2002). Precocial species do not feed their young

and therefore the food availability in the environment might have different (or weaker) effect on their allocation decisions if compared to altricial species. Their geographical distribution may thus more strongly reflect the distribution of specific breeding habitats than spatial variation in food availability (Clark and Shutler 1999, Bloom et al. 2013). Moreover, most altricial species rely mainly on resources collected directly from the environment during breeding (income breeders) and thus they have to adjust their investments into clutch size according to presumed future demands for feeding their young (Jönsson 1997). On the contrary, precocial birds frequently use energetic reserves in the form of body fat (capital breeders) and do not feed their young after hatching (Ricklefs 1968, Bennett and Owens 2002). As a consequence, reproductive investment in precocial birds might not reflect too much the actual food availability during breeding, as in altricial birds, but also seasonality in food supply. Furthermore, the young in precocial species are more developed after hatching in comparison to altricial species, and females thus invest energy into production of yolk-rich eggs, which potentially constrains clutch size (Starck and Ricklefs 1998). This is especially the case of precocial species living in sub-arctic regions, where young have to be highly developed and almost totally thermally independent after hatching to survive the harsh environmental conditions (Koskimies and Lahti 1964).

As precocial species form ecologically a very diverse unit, the geographical patterns in reproductive traits can be to some extent caused by the predominance of particular groups of precocial birds in a given area. For instance, Charadriiformes and diving ducks dominate in the north, while Phasianidae and dabbling ducks occur rather in the middle of the continent. However, it still may reflect the fact that some environmental conditions are more suitable for particular avian groups with specific reproductive traits than for the other groups. Environmental conditions select and/or filter avian traits, and the abovementioned distribution of major bird groups may be a consequence of this filtering. Also, many precocial species are waterbirds and the level of productivity in water habitats may not be connected with productivity in surrounding area estimated here by NDVI. This could significantly contribute to the different spatial patterns between precocial and altricial birds. Additionally, some of precocial species have been under strong hunting pressure during last centuries which could modify their distributional ranges (Keane et al. 2005).

The relatively low proportion of explained variation in clutch size of altricial birds can also reflect the fact that avian traits might be constrained by other factors. Ricklefs and Wikelski (2002) argued that individual adaptive responses to different environments are limited by physiological mechanisms, namely that endocrine control mechanisms produce incompatible physiological states that restrict variation in life-histories. Indeed, hormonal levels were identified as correlates of crucial life history traits in birds (Hau et al. 2010). Other more ultimate factors could include incubation ability of parents (Lack 1948, Hills 1980), allocation of limited resources into competition or predator avoidance (Cody 1966, Skutch 1985) or the capacity of parents to provide protection to their young against predators (Safriel 1975). Alternatively, the discrepancy between spatial

patterns observed in altricial and precocial birds might be caused by the fact that the group of altricial birds includes an ecologically homogeneous clade of Passerines (Claramunt and Cracraft 2015), but precocial birds differ markedly in many respects. They have pronouncedly different feeding strategies (Sekercioglu et al. 2004), mating behaviour (Temrin and Tullberg 1995) or nesting (Collias 1964). As a consequence, the spatial patterns in their reproductive traits might be masked by inter-taxa differences in other ecological adaptations. However, we did not find striking differences between the models based on raw data and data controlled for taxonomy. These effects thus do not seem particularly important.

In our analyses, we focused on European birds, which however, represent only a part of the avian life-history spectrum. Tropical species would add more variation in life-history traits and it is possible that life-histories of birds in tropical areas are shaped by different factors than in the temperate zone. To describe reproduction, we used information about investment into a current breeding attempt or a single breeding season. Obviously, life-time reproductive investment would better inform about the avian life-history, however, such data are unavailable (e.g. due to the lack of life span information). In this study, we expect that current reproductive investment is optimised similarly as life-time reproductive investment and they are correlated. Assuming that the life expectancy is comparable among ecologically similar species in Europe, our expectation is reasonable. The situation might be, however, different for comparison of temperate and tropical birds.

In conclusion, we detected clear spatial patterns in assemblage means of avian reproductive traits across Europe, although lack of data prevented us from accounting for the intra-specific variability of avian traits, so that the real geographical variation in reproductive parameters might be slightly different. We found relatively weaker geographic patterns in precocial species than in altricial ones. In altricial passerines, latitude was the strong determinant of variation in clutch size and the number of broods, while the overall reproductive investment was related mostly to longitude. In agreement with our predictions, we found that large clutch sizes dominated in areas with high environmental productivity, while high number of broods was typical in areas with long breeding season. Additionally, we found that precocial species have large clutch sizes in areas with high annual seasonality, but, in contrast to our expectations, we did not corroborate this in altricial species. Moreover, we showed that high number of broods dominate in areas with low annual seasonality as we predicted, but this effect was significant again only in precocial, and not in altricial species. In addition, our data provide a large scale correlative evidence for a possible trade-off between clutch size and the number of broods in altricial species. Results concerning overall reproductive investment showed a picture consistent with our predictions: it was high in highly productive areas with long breeding season and low annual seasonality. Overall, altricial birds seemed to be influenced mainly by food availability and the length of the season, while seasonality was as much important in precocial birds.

Acknowledgements – We are grateful to Petr Keil for valuable comments during early stages of the project. Comments of the editor greatly improved the manuscript.

Funding – The research was supported by the Czech Science Foundation (projects no. P505/11/1617 and GB14-36098G) and by the European Union FP7 SCALES project ('Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal, and Ecological Scales'; project 226852).

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Supplementary material (Appendix JAV-01131 at <www.avianbiology.org/appendix/jav-01131>). Appendix 1–3.