Effects of urbanization on bird phenology: a continental study of paired urban and rural populations

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ABSTRACT: Urban habitats differ from adjacent natural habitats in terms of disturbance regimes, light, temperature, rainfall, habitat distribution and resource abundance. Meteorological differences advance and prolong the growing season in urban habitats compared to nearby rural areas. In turn, urban bird populations may potentially start singing earlier, and reproduce earlier and more frequently than rural populations. However, this prediction has previously only been tested with data from single species using single spatial replicates from rural and urban sites. Here we provide the first general (paired urban and rural populations of 54 bird species) and large-scale (a 3800 km long latitudinal gradient across Europe) empirical evidence for longer and earlier singing periods in urban compared to rural habitats. Effects of urbanization on start and duration of the singing period (as a proxy for the breeding season) were positively related to size of cities and ecological characteristics of species. Bird species that have been urbanized for a long time started to sing earlier and had a more extended singing period in urban compared to rural habitats. We also found that the singing period started later and was shorter at higher latitudes. Geographical variation in phenology was related to temperature and rainfall, although differences between urban and rural habitats were not. Differences in duration of singing periods between paired urban and rural sites were as large as latitudinal differences between southern and northern Europe (5, 6 and 28 d for 3 common species, as compared to a mean latitudinal variation of 17.1 d). This suggests local adjustment to urban environments, either due to evolution or to plasticity of phenological behaviour.

KEY WORDS: Singing periods · Phenology · Population density · Urbanization

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1. INTRODUCTION

Conversion of natural habitats into urban settlements represents one of the major ecological changes in our world (Grimm et al. 2008). When urban habitats become colonized by many organisms, urbanization becomes an ideal model system for invasion ecology (Evans 2010, Møller et al. 2012, 2015, Díaz et al. 2013). Urban habitats differ from more natural (including rural) habitats in terms of disturbance regimes, light, temperature, rainfall, habitat heterogeneity and distribution, and resource abundance (Gilbert 1989, Rebele 1994, Turner et al. 2004, Alberti 2005, Miller 2005, Small et al. 2007). This implies a strong selection pressure on animals in their novel urban environments. Therefore, urban populations are expected to deviate from rural counterparts in their physiological, behavioural and life-history traits, and these differences have been empirically supported (Partecke et al. 2004, 2005, 2006, Partecke & Gwinner 2007). However, despite previous research on urban birds at the community level, behavioural and ecological studies in urban environments are still rare (Marzluff et al. 2001, Bonier et al. 2007, Díaz et al. 2013, Samaš et al. 2013a, Gil & Brumm 2014).

Previous studies that addressed the question of how urban birds differ from rural conspecifics in their breeding parameters were often based on data from a single species and a single spatial replicate per rural and urban site (e.g. Partecke & Gwinner 2007, review in Deviche & Davies 2014). Although such studies suggested specific patterns and mechanisms and contribute to our knowledge of urbanization effects on animals, they cannot exclude the possibility that single model species or single pairs of urban-rural sites (Partecke et al. 2006) are not representative of general patterns but reflect local effects, or 'location differences' sensu Hurlbert (1984). To be able to generalize from local results it is necessary to include spatial replicates (Evans et al. 2009), taxonomic replicates (Møller 2008a,b, 2009, Polačiková & Grim 2010), or both (Møller 2008a,b, 2009, 2010, Grim et al. 2011, Samaš et al. 2013a). Replication of whole studies, i.e. meta-replication, is the only way to achieve scientific generalizations (Johnson 2002). Therefore, here we followed a spatial-taxonomical replication approach by studying whole breeding communities across a large geographical scale in Europe, covering the entire north-south range for most species included in the analyses. Using this approach we have previously shown general patterns of positive covariation between breeding density and time since urbanization (for a full expla-

nation, see Section 2 and Møller et al. 2012), and consistently different antipredator behaviour of birds in urban versus rural areas (Díaz et al. 2013, see also Møller et al. 2013). In the present study we focused on differences in the most conspicuous and typical aspect of avian breeding behaviour between urban and rural habitats — the phenology of singing activity.

The survival of any species in urban environments is dependent on physiological (Partecke et al. 2005) and behavioural (Díaz et al. 2013) changes that permit adjustment to changes in the environment (Gil & Brumm 2014). One of the most important adjustments concerns reproduction, which must be timed to occur during the period that assures maximum probability of survival for young and their parents. Therefore, the optimal timing of the start and duration of the singing period will be important determinants of reproductive output and the number of annual breeding attempts for species colonizing new environments. Because of generally better food availability (Deviche & Davies 2014), higher temperatures (urban heat island phenomena; e.g. Landsberg 1981, Gilbert 1989) and higher rainfall (Small et al. 2007), as well as artificial lights that interfere with changes in the natural photoperiod, the breeding season (including the start of singing and the duration of the singing period) is predicted to be longer in urban than in rural habitats (Deviche & Davies 2014). Although several studies have addressed this hypothesis, all lack the level of replication needed to generalize results. Deviche & Davies (2014) recently listed 17 such comparisons of phenology between an urban and a rural population. Although 12 of these 17 comparisons showed earlier laying in urban habitats, 4 were on great tits *Parus major*, 3 on blue tits *Cyanistes caeruleus*, and 2 each on black-billed magpies *Pica pica*, starlings *Sturnus vulgaris* and house sparrows *Passer domesticus*; thus only 9 species were considered by these studies. Even these 9 species cannot be considered statistically independent because the similarity in response by great and blue tits may potentially reflect common phylogenetic descent. Furthermore, these 9 species are unlikely to constitute a random sample. This calls for the systematic study of all species at a large scale while addressing the potential statistical dependence of such data on common phylogenetic descent rather than convergent evolution.

Some species are better able to live and colonize urban habitats than others (Klausnitzer 1989, Gliwicz et al. 1994, Stephan 1999, Anderies et al. 2007, Møller 2009, 2010). Species living a long time within

and strongly preferring urban environments such as feral pigeons *Columba livia* f. *domestica* and house sparrows ('urban exploiters'; Blair 1996), or species that now have much higher population densities in urban than rural distribution areas ('urban adaptable species'; Blair 1996) such as blackbirds *Turdus merula*, are regarded as successfully urbanized bird species. Because of adjustment to changing environmental conditions due to urbanization, they may start reproduction earlier and their breeding season may be longer than that of other species (Stephan 1999). Although breeding seasons, and hence singing periods of birds, have been stated to be earlier and longer in urban than in rural populations (Klausnitzer 1989, Gliwicz et al. 1994, Stephan 1999, Deviche & Davies 2014), we are unaware of any study that actually demonstrates such an effect based on a spatially and taxonomically replicated design that also accounts for potential geographic and phylogenetic effects.

We assess the extent to which urbanization has affected the timing (start) and the duration of singing and hence reproduction, using birds in European cities as a model system. We employ the duration of the singing period as a surrogate for the breeding season (for validation of this approach see 'Methods'). It has earlier been suggested that behavioural plasticity in singing behaviour may allow species to adapt to environments changed by humans (Slabbekoorn & den Boer-Visser 2006, Díaz et al. 2011). We expected that species that have been urbanized for a long time, or species that have relatively higher population density in urban habitats, would start to sing earlier and have longer singing periods than species that have only recently colonized urban areas (e.g. wood pigeons *Columba palumbus*). We also hypothesize that the size of cities may affect the timing of urbanization, if a larger city provides more opportunities for urbanization (see the 'target effect' in island biogeography) and a higher success rate of urbanization (increasing patch area decreases the risks of extinction, other things being equal).

Both species and study sites may differ in important ecological attributes that directly or indirectly affect the estimate of duration of the singing period. We quantified the effects of body size, winter territoriality, colonial breeding and migration. Body size was included because large species have lower population densities and smaller total population sizes than small species (Greenwood et al. 1996). Several species such as resident populations of robins *Erithacus rubecula* defend winter territories by singing, potentially leading to a biased estimate of the duration of the breeding season based on the duration of the annual singing period. Colonial breeding may affect the probability of establishment in urban habitats because simultaneous immigration by multiple individuals will increase the probability of successful establishment. Annual migration between breeding and wintering areas is associated with longer dispersal distances and a low degree of phylogenetic divergence among populations (Paradis et al. 1998). Hence, migration could act as a factor preventing or reducing the probability of successful colonization of urban habitats. Nevertheless, singing (and breeding) periods in urban bird populations can still be expected to be earlier and longer than in rural ones after accounting for these life-history effects, and this prediction should be robust to geographic and phylogenetic effects that potentially affect the duration of singing periods. Regarding sites, latitudinal and urban/rural effects on temperature and rainfall may influence singing behaviour of birds by acting as cues to adjust the timing of reproduction to optimal conditions (Deviche & Davies 2014). We gathered data on spring temperature and rainfall at study sites to analyse whether latitudinal and urban/rural changes in reproductive phenology were correlated with spatial changes in these environmental cues.

2. METHODS

2.1. Research team

Our research team was established in 2009 to analyze the causes and consequences of avian urbanization. We follow an explicit spatial-taxonomical replication approach by studying whole breeding communities across a large geographical scale, covering the entire north-south range of most species included in the analyses. We have already addressed how breeding density covaries with time since urbanization (Møller et al. 2012), and how antipredator behaviour is related to urbanization (Díaz et al. 2013).

2.2. Study areas

We studied the duration of the singing period in 2009 in 8 cities (each paired with a nearby rural area) across Europe, from Granada and Paris in the southwest to Rovaniemi and Tallinn in the northeast (Fig. 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/c066p185_supp.pdf), using consistent methods (see below) across all spatial replicates. Cities were selected to cover, as far as possi-

Fig. 1. Location of 8 paired localities with urban and rural study sites for a large-scale study of singing dates of birds

ble, the widest latitudinal and longitudinal gradients in Europe. The distance between urban and paired rural study sites was 1–20 km, depending on the availability of similar urban and rural sites in terms of general altitude and habitat types (see next paragraph). The benefit of this approach is that neighbouring study sites will likely share most characteristics including e.g. general weather, altitude and soil, and individual birds will not be prevented from moving between neighbouring urban and rural habitats because of the distance between sites. The size of cities was estimated as their human population sizes (extracted from www.wikipedia.org; Table S1), which are strongly positively correlated with estimates of the surface area of cities ($r_s = 0.98$, p < 0.001). A large city will have a larger population of birds, and hence the probability of colonization and the subsequent probability of extinction are likely to vary with size. We controlled statistically for the effects of latitude, longitude and human population size on timing and duration of the singing period in the subsequent analyses.

All urban study sites included areas with multi-storey buildings, single-family houses, roads and

parks, while nearby rural areas had open farmland and woodland and did not contain continuous urban elements like multi-storey buildings, single-family houses, roads or parks. This simple operational definition is also adopted in other studies (e.g. Klausnitzer 1989, Gliwicz et al. 1994, Stephan 1999), and our definitions of urban (percent of built-up area >50, building density >10 ha^{-1}, population density >10 ha^{-1}) and rural habitats (percent of built-up area 5 to 20, building density <2.5 ha^{-1}, population density 1 to 10 ha^{-1}) follow Marzluff et al. (2001). Site classifications were carried out based on maps followed by field visual assessment of these traits. We based classifications on site characteristics rather than distances to a hypothetical 'city border' since the limits of cities are blurred to a variable extent among cities as a result of their development histories, among other reasons. Recent papers aimed at developing quantitative estimates of the degree of urbanization show high consistencies between these semi-qualitative classification criteria and more sophisticated semi-automated scoring methods (e.g. Seress et al. 2014).

2.3. Ecological characteristics of populations and species

Mean body mass of adult birds (log$_{10}$-transformed to approach a normal distribution) of each species was taken from Cramp & Perrins (1977–1994). We classified all populations with respect to 3 ecological factors, taking account of the fact that such characteristics differed among populations (e.g. robins have winter territories in Paris, while they are migrants in Tallinn).

Winter territoriality. Populations with individuals that sing during winter to defend feeding territories and/or roosting sites were classified as winter territorial, and all other species as not being winter territorial (Cramp & Perrins 1977–1994). Species with winter territories will by definition have longer singing periods than species with no winter territories.

Colonial breeding. We classified all species as solitary or colonial, with species with aggregated nest sites and small breeding territories without food resources being classified as colonial, and all other species as solitary. Colonial species generally compete intensely for breeding sites (Lack 1968), a fact that likely selects for earlier start of singing in spring and later termination in summer.

Migration. We classified all populations as residents or migrants (migrating between Europe and North Africa, or across the Sahara; Cramp & Perrins

1977–1994). Partial migratory populations were listed as migratory. Migrants were expected to have shorter singing periods because they arrive late in spring, and because migrants are less common in urban habitats (Partecke & Gwinner 2007), and this could potentially confound any effects of urbanization on phenology of singing.

2.4. Urbanization: timing and density

We tested for the potential effects of timing of urbanization, estimated as the difference in population densities between paired urban and rural sites. This measure can be obtained for all species in all sites, and it was closely related to the available estimates of the time at which each species became urbanized at several of our study cities (see Møller et al. 2012 for a full explanation). Relative population density in urban versus rural habitat was measured as the $\log_{10}$-transformed population density in urban areas minus the $\log_{10}$-transformed population density in paired rural areas (with an added constant of 0.01 to avoid problems with a few population density estimates of zero). Detailed explanations of how we obtained these estimates, as well as why detectability effects would not have biased results on the basis of paired comparisons, are given in Møller (2008a, 2009, 2010) and Møller et al. (2012).

2.5. Weather and climate gradients

We obtained data on mean temperature and total rainfall for the 3 spring months (March, April and May) and for the whole 3 mo spring period from public databases (Table S2 in the Supplement). We selected the main weather stations located in each study city and the stations located in the closest small towns or airports that would estimate weather conditions in the rural areas surrounding cities, as weather stations were not always available close to study sites. Data were recorded from both the study year and from the longest time series available (usually the last 30 yr period), except for Tallinn and Olomouc rural stations (Table S2).

2.6. Start and duration of the singing period

To estimate start and duration of the singing period both in urban and rural environments we followed established and recommended standard protocols (see Voříšek et al. 2010). We employed the line transect method conducted weekly during spring, summer and fall 2009. Three to 5 km line transects were selected using a stratified random sampling design to ensure that all locally available habitats were included and that their proportion was similar between urban and rural sites within each pair (Møller et al. 2012). We were unable to use multiple routes or place routes entirely randomly in some of our study sites, especially in smaller urban areas, as it was impossible to enter private land, factories, or large built-up areas. Line transects were traversed by the same person in urban and rural areas within each pair of urban and rural study sites in the morning (before local sunrise until 10:00 h, as recommended by Voříšek et al. 2010). We always started line transects before the start of avian singing activity (owls excluded) based on our experience for each particular study population (Kempenaers et al. 2010). Surveys in urban and rural sites were conducted on 2 consecutive mornings each week, starting alternately with the urban and the rural transect. We recorded all singing birds and all birds seen or heard along the route without any distance limit (following Voříšek et al. 2010).

We attempted to avoid possible effects of stochastic variation in weather conditions on bird singing by conducting surveys on consecutive mornings and only during good weather conditions. We recorded not only 'singing' individuals, i.e. the territorial songs of oscine passerines, but also vocalizations such as cooing calls of pigeons, flight calls of swifts, and the territorial calls and drumming behaviour of woodpeckers, as these sounds have similar functions as song in oscine passerines (Cramp & Perrins 1977–1994).

We estimated duration of the singing period in urban and rural habitats in 2 ways. First, we estimated mean and standard deviation of singing date (i.e. ordinal date in the year) for all species, localities and habitats, using all dated singing records. The standard deviation is larger when the duration of the singing period is longer. Second, we estimated 10th and 90th percentiles of the singing date for all species, localities and habitats (urban vs. rural). We used these percentiles and not the original data ranges to avoid problems of sampling at the tails of frequency distributions (outliers). The results of tests of consistency in estimates, consistency in estimates among years for one of the study sites, and consistency in estimates based on singing records and records of nests, eggs and fledglings based on published information or our own data are provided in Text Section S1 of the Supplement.

We acknowledge that timing of singing is only a correlate of timing of breeding; the surrogate nature of our timing of the breeding season inevitably increases noise in our analyses. Consequently, only strong patterns could be detected, making our conclusions conservative.

2.7. Statistical analyses

We tested for differences in mean and variance in singing date using Levene's test for equality of variances followed by Welch's ANOVA for unequal variances. We identified 137 pairs of urban and rural populations of 54 species that fulfilled the criterion of a minimum of 20 observations of singing individuals in each population. We tested if species were consistent in phenology by using species as a factor. We developed full models of the relationship between date of singing (continuous response), city and species as random factors, habitat (urban vs. rural) as a fixed factor, and their 2 and 3-way interactions as predictors. Higher order interactions that were not significant (p > 0.05) were sequentially eliminated from the model. Finally, we analyzed differences in phenology between urban and rural habitats (response variables), while using latitude, longitude, mean temperature, rainfall, size of city, winter territoriality (yes vs. no), colonial breeding (colonial vs. solitary) and migration (migrant vs. resident) as predictor variables and controlling for potential multicollinearity (estimated with VIF analysis; for details see Zuur et al. 2010).

Observed phenological responses to predictor variables can be influenced by the phylogenetic relationships among the species sampled that are not statistically independent estimates of such responses due to common ancestry. To control for such relationships we used phylogenetic generalized least square regression (PGLS) models implemented in R (see Díaz et al. 2013 for a similar approach). After estimating the phylogenetic scaling parameter lambda (λ), we calculated the phylogenetically corrected partial correlations between the variables of interest. Different populations of the same species were considered as polytomies with a constant small genetic distance of 1×10^{-10} between them. We used the R script and the edited phylogeny supplied as Supplementary Files S1 and S2 in Díaz et al. (2013), but using the function *pglm3.3.r* instead of the *pglm3.1.r* in the script and including a polytomy for 2 common swift *Apus apus* populations in the phylogeny.

3. RESULTS

3.1. Song period and urbanization

Examples of annual patterns of singing for 4 bird species out of a total of 137 pairs of rural and urban populations are shown in Fig. 2. Urban populations started singing earlier and finished later than nearby rural populations (Table 1). There were highly significant effects of species for all phenological variables for urban and rural habitats. In the analysis of difference in estimates between urban and rural habitats only the 10th percentile showed a statistically significant effect of species (Table 1).

Latitude was not significantly related to the 10th percentile ($F = 3.45$, df = 1,132, p = 0.07, slope = 0.51 ± 0.27 [SE]), 90th percentile ($F = 0.07$, df = 1,132, p = 0.80, slope = −0.08 ± 0.32 [SE]), mean singing date ($F = 0.01$, df = 1,132, p = 0.93, slope = 1.51 ± 0.33 [SE]), or duration of the singing period ($F = 2.23$, df = 1,132, p = 0.14, slope −0.59 ± 0.40 [SE]), in models that also included body mass, migration, winter territoriality and coloniality as predictor variables. Interestingly, these results changed after phylogenetic correction, showing that birds started the singing period later (10th percentile) and that it was shorter at higher latitudes ($F = 5.82$, df = 6,137, p = 0.017, slope = 0.08 ± 0.03 [SE] and $F = 8.24$, df = 6,137, p = 0.005). Results for mean singing date and for the 90th percentile did not change ($F = 0.02$ to 0.29, p = 0.15 to 0.59).

An analysis of all records of song dates between urban and rural habitats revealed a highly significant difference in mean date (Welch's test: $F = 27.03$, df = 1,19653, p < 0.0001), with the mean ordinal date being 160.82 for rural areas and 166.03 for urban areas. There was also a highly significant difference in variance as revealed by Levene's test ($F = 186.50$, df = 1,19965, p < 0.0001), with the variance being significantly larger for urban than rural areas (2580.64 vs. 1957.18). A model of singing dates based on all singing records revealed significant effects of city and species, as well as interactive effects of both factors with habitat (Table 2).

The duration of the singing period in urban habitats increased with the duration of the singing period in rural habitats ($F = 181.17$, df = 1,135, $r^2 = 0.57$, p < 0.0001, slope = 0.789 ± 0.059 [SE]), with the intercept being significantly larger than zero (19.6 ± 5.53 d [SE], $t = 3.54$, p = 0.0005). Thus, urban singing periods were predicted to last 20 d when the duration in rural areas was zero. The slope was significantly smaller than one ($t = 3.60$, df = 135, p < 0.0001), implying that species with long singing periods had relatively shorter peri-
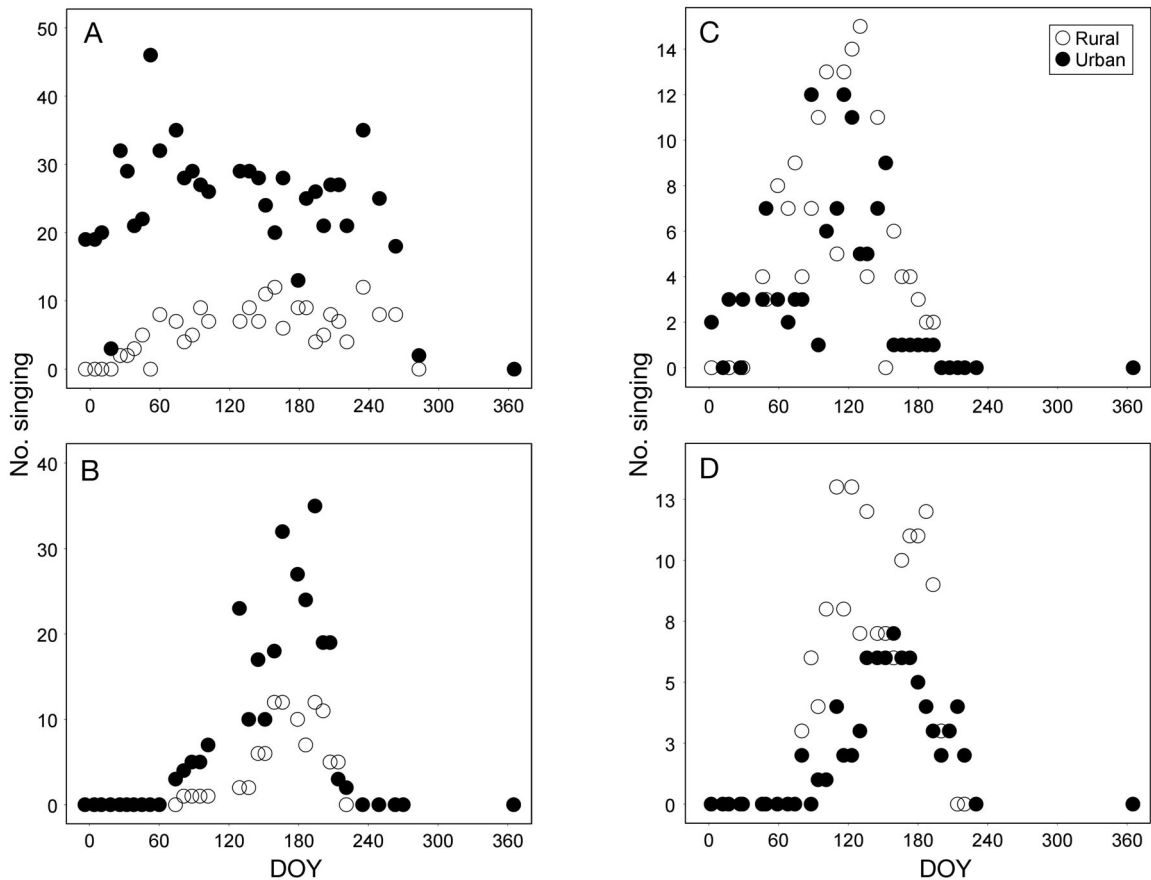
Fig. 2. Examples of annual patterns of singing in urban and rural populations of (A) wood pigeon *Columba palumbus* in Brønderslev, Denmark, (B) blackbird *Turdus merula* in Brønderslev, Denmark, (C) great tit *Parus major* in Orsay, France and (D) blackcap *Sylvia atricapilla* in Orsay, France. Note that the first 2 species have higher density in urban habitats while the latter 2 species have higher density in nearby rural habitats. DOY: day of the year

ods in rural than in urban habitats. Thus, urbanization particularly benefitted species with relatively short singing periods. These results did not change after inclusion of species as a predictor because species effects were not significant ($F = 1.38$, df $= 53, 82$, p $= 0.09$).

Differences in mean singing date between urban and rural habitats were statistically significant at the 5% level in a total of 31 pairs, deviating significantly from the null expectation of 6.85 pairs (5% out of a total of 137 comparisons: $G = 21.76$, df $= 1$, p < 0.0001). Of these 31 differences, 19 showed later singing in rural than in urban habitats and 12 later singing in urban than in rural habitats. Twenty-five Levene's tests for similar variance in urban and rural habitats were

Table 1. Summary statistics for mean, 10th and 90th percentiles and standard deviation in singing date of pairs of urban and rural populations of different bird species. N = 137 pairs of populations (54 species). 'Effect of species' refers to species as a factor in a 1-way analysis of variance with the 5 variables as response variables. Dates are ordinal dates with 1 = January 1. *p < 0.05, ***p < 0.0001

Variable	Urban mean	Urban SD	Effect of species (F)	Rural mean	Rural SD	Effect of species (F)	Urban– rural mean	Urban– rural SD	Effect of species (F)
Mean date	124.26	27.67	3.55***	125.93	27.01	3.30***	−1.67	13.67	1.33
10th percentile	82.36	34.77	5.33***	85.00	33.22	5.86***	−2.64	16.59	1.67*
90th percentile	169.81	30.08	2.74***	171.00	27.14	2.69***	−1.19	20.65	1.27
10th to 90th percentile	87.45	40.69	2.34***	86.00	39.04	2.60***	1.45	27.84	1.22
Standard deviation in date	32.45	14.33	2.56***	32.55	15.11	2.67***	−0.10	9.46	0.87

Table 2. Model of the relationship between singing date and city, species (random factor), habitat (fixed factor) and their 2-way interactions in an analysis based on all individual singing records. The model had the statistics $F = 29.27$, df = 200,19451, $r^2 = 0.22$, p < 0.0001. Effect sizes are reported as partial eta-squared statistics. *p < 0.05, **p < 0.01, ***p < 0.0001

Variable	Sum of squares	df	F	Effect size
City	368470	7	2.65*	0.21
Species	3281423	53	4.14***	0.67
Habitat	2436	1	0.83	0.02
City × Species	2365859	79	16.50***	0.06
City × Habitat	46689	7	3.67**	0.01
Species × Habitat	221671	53	2.30***	0.01
Error	35302131	19451		

statistically significant, deviating significantly from the null expectation of 6.85 (5% out of a total of 137 comparisons: $G = 13.50$, df = 1, p < 0.0001). Of these 25 differences, 10 showed larger variance in singing date in rural than in urban habitats and 15 larger variance in urban than in rural habitats.

The difference in mean date of singing was not significantly correlated with the difference in variance in date of singing ($F = 0.65$, df = 1,135, $r^2 = 0.00$, p = 0.65), so when the variance in singing date increased in urban relative to rural habitats, there was no change in difference in mean singing date. This result did not change after phylogenetic correction ($\lambda = 7.9 \times 10^{-5}$, $F = 1.02$, p = 0.31). There was no significant relationship between difference in mean singing date between urban and rural habitats and difference in population density between urban and rural habitats (Fig. 3A; $F = 0.01$, df = 1,135, p = 0.92 after phylogenetic correction). In contrast, there was a significant positive relationship between difference in 10th to 90th percentile singing period between urban and rural habitats and difference in population density between urban and rural habitats (Fig. 3B). This relationship remained significant after phylogenetic correction ($F = 11.10$, df = 1,135, p = 0.001).

The difference in mean singing date between urban and rural habitats increased with human population size (Fig. 4, Table 3). Birds in large cities started to sing later relative to those in nearby rural areas whereas birds in smaller towns started to sing earlier relative to those in paired rural localities.

3.2. Singing period and ecological variables

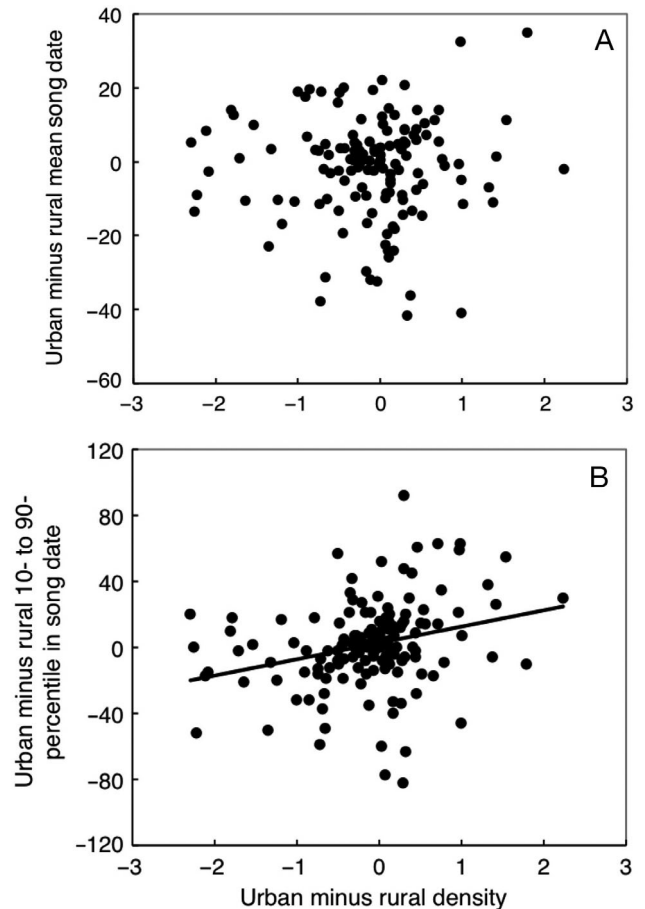Singing phenology was significantly related to winter territoriality. Species with winter territoriality

Fig. 3. Difference in (A) mean singing period and (B) 10th minus 90th percentile singing period between urban and rural populations of different bird species in relation to difference in population density. The linear regression line is shown in (B); in (A) the relationship was not significant. The 2 models had the statistics $F = 0.02$, df = 1,135, $r^2 = 0.00$, p = 0.88 and $F = 10.70$, df = 1,135, $r^2 = 0.07$, p = 0.0014, respectively
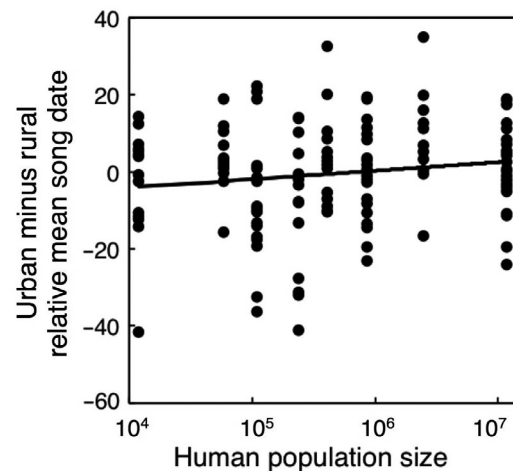

Fig. 4. Difference in mean singing date between urban and rural populations of different bird species in relation to human population size of cities. Solid line: linear regression

Table 3. Difference in phenological variables between urban and rural habitats in relation to geographical position, human population size and ecological variables in an analysis of 137 pairs of bird populations. Values are partial effects from the full model that included the 6 predictors listed in the table. The full models had df = 6,130. Slopes (effect sizes) of significant partial effects are also shown, as well as the *F* and slope values for these significant effects. Results did not change after phylogenetic correction since the phylogenetic scaling parameter λ did not differ from zero (p = 1) in any of the phylogenetically corrected analyses. AIC: Akaike's information criterion. *p < 0.05, **p < 0.01, ***p < 0.0001

Variable	°N	°E	Human population size	Winter territoriality	Colonial breeding	Migration	Model *F*	Model AIC
Difference in mean singing date	1.53	0.62	7.05** 3.37	9.54** −5.93	0.26	0.73	3.08**	716.9
Difference in 10th percentile	0.21	2.11	0.63	10.36*** 7.49	3.80* −4.45	1.25	2.75**	770
Difference in 90th percentile	1.23	0.04	3.23	5.07* −6.42	3.98* 5.58	0.02	2.62**	828.6
Difference in 10th minus 90th percentile	1.17	0.51	0.69	0.07	6.82** 10.03	0.31	1.97*	915.6

started singing earlier in urban than in rural habitats compared to other species, as reflected by a difference in 10th percentile. This effect amounted to a mean difference of 10 d. However, this effect was countered by earlier termination of singing in urban compared to rural habitats, as reflected by the difference in 90th percentile (Table 3). This effect amounted to a mean difference of 9 d. Therefore, birds in urban populations on average sang 9 d earlier than birds in rural populations (Table 3).

Difference in phenology between urban and rural habitats was significantly related to breeding sociality. The difference in 10th percentile was negatively related to colonial breeding, with colonial species on average starting to sing 8 d earlier than solitary breeders in urban compared to rural habitats (Table 3). In addition, the difference in 90th percentile was greater between habitats in colonial than in solitary species, with colonial species finishing singing on average 7 d later in urban than in rural habitats. Therefore, the difference in duration of the singing period was larger in colonial species, with colonial species singing for 16 d more than solitary species. Finally, migratory habits had no general consequences for singing phenology (Table 3).

3.3. Weather and climate gradients

Mean monthly and spring temperature in 2009 were closely positively correlated with the long-term temperature values across study sites (r_{14} = 0.895 to 0.992, p < 0.0001), and mean monthly values were strongly positively correlated both between months and with the whole-spring average (r_{16} = 0.835 to 0.962, p < 0.0001 for 2009 and r_{14} = 0.954 to 0.999, p < 0.0001 for long-term values). In contrast, monthly and spring rainfall were weakly or not significantly correlated with long-term rainfall values (r_{14} = −0.046 to 0.553, p = 0.88 to 0.050), whereas monthly values were correlated with overall spring rainfall (r_{16} = 0.621 to 0.759, p = 0.01 to 0.001 and r_{14} = 0.804 to 0.981, p < 0.001 for 2009 and long-term values, respectively), but not, generally, among them (r_{16} = 0.251 to 0.300, p = 0.38 to 0.26 and r_{14} = 0.402 to 0.823, p = 0.15 to 0.001 for 2009 and long-term values, respectively).

Mean spring temperature decreased significantly northwards across study sites ($F_{1,23}$ = 231.42, p < 0.0001), with no significant main or interactive effects of rural/urban (i.e. heat island effects) or recording period (2009 or long-term data; general linear model [GLM], $F_{1,23}$ = 0.00 to 2.92, p = 1.000 to 0.101; Fig. S1 in the Supplement). City size had no effects of rural-urban lack of differences ($F_{1,14}$ = 0.45, p = 0.514 for the habitat × city size interaction in a model including log(city size) as an additional predictor variable). Spring rainfall did not show any significant linear trend with latitude, nor main or interactive effects of rural/urban or recording periods (GLM, $F_{1,23}$ = 0.05−1.08, p = 0.821 to 0.310; Fig. S1). The same qualitative results were obtained when using monthly values of temperature and rainfall.

The singing period started earlier at higher temperatures and higher rainfall, while the duration of the singing period increased with higher temperatures and higher rainfall in 2009 in models that also included body mass, migration, winter territoriality and coloniality as predictor variables. The 10th percentile was negatively correlated with mean tem-
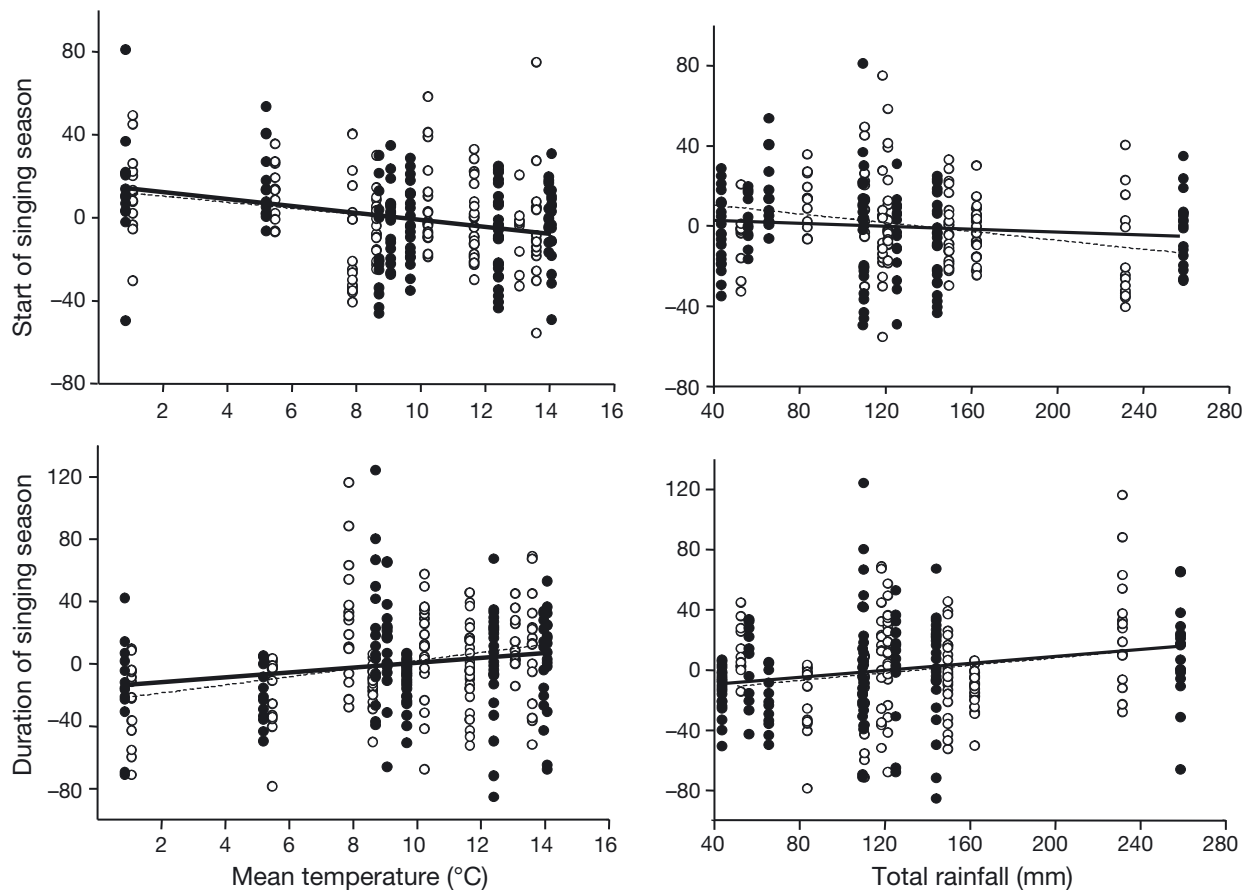
Fig. 5. Start and duration of the singing periods in 137 pairs of bird populations (54 species) in relation to mean temperature and spring rainfall. (●) urban populations; (○) rural populations. Phenological parameters are residuals from models relating 10th percentile and 10th minus 90th percentile singing period in relation to body mass, migration, winter territoriality and coloniality. Lines (continuous: urban; dashed: rural) are best-fit linear regressions

perature and total rainfall in both urban ($F = 12.07$ and 1.74, df = 1,131, $p < 0.05$, slopes [±SE] = −1.70 ± 0.49 and −0.04 ± 0.03 for temperature and rainfall, respectively) and rural populations ($F = 10.79$ and $F = 9.52$, df = 1,131, $p < 0.002$, slopes [±SE] = −1.65 ± 0.50 and −0.11 ± 0.04). The duration of the singing period was positively correlated with increasing temperature and rainfall (respectively, $F = 5.48$ and 8.03, df = 1,131, $p < 0.02$, slopes [±SE] = 1.70 ± 0.73 and 0.12 ± 0.04 for urban and $F = 15.07$ and 5.86, df = 1,131, $p < 0.02$, slopes = 2.90 ± 0.75 and 0.13 ± 0.05 for rural populations). The 90th percentile was positively, although weakly, correlated with rainfall for urban populations ($F = 4.93$, df = 1,131, $p = 0.028$, slope = 0.08 ± 0.04). Mean singing dates were not significantly correlated with any weather variable ($F < 1.90$, $p > 0.17$). These results were the same after phylogenetic correction ($\lambda < 7.15 \times 10^{-5}$, $\chi^2 < 0.006$, p ~1.00). Thus, the singing period was

longer at localities with warmer and more humid springs mostly because of an earlier start of singing (Fig. 5).

Weather variables were not correlated with phenological differences among paired urban and rural sites. The incorporation of both means and differences between urban and rural sites in mean spring temperature and total rainfall in 2009 in the models of Table 3 did not improve them significantly (Akaike information criterion [AIC] = 719.2, 770.7, 834.3 and 918.5 for the models incorporating mean differences in spring temperature and rainfall, ΔAIC = 2.2, 0.7, 5.6 and 3.0 for differences in 10th percentile, 90th percentile, mean dates and durations, respectively). In addition, effects of weather variables in models were not significant and their inclusion did not change the pattern of significance of the other factors (data not shown). These results did not change after phylogenetic correction since the

Table 4. Estimated increase in number of annual breeding cycles in urban compared to rural populations of wood pigeon *Columba palumbus*, blackbird *Turdus merula* and house sparrow *Passer domesticus*

Variable	Columba palumbus	Turdus merula	Passer domesticus
10th percentile of singing period in urban habitats (DOY)	71	84	62
90th percentile of singing period in rural habitats (DOY)	79	79	77
Duration of breeding season in urban habitats (d)	127	95	111
Duration of breeding season in rural habitats (d)	122	89	83
Difference in duration of breeding season (d) between urban and rural habitats	5	6	28
Duration of a single breeding cycle (d)	60	35	35
Increase in number of breeding cycles between urban and rural habitats	0.08	0.17	0.80

phylogenetic scaling parameter λ did not differ from zero (p = 1) in any of the phylogenetically corrected analyses (data not shown).

3.4. Fitness consequences of urbanization and breeding season

We attempted to estimate the fitness consequences of earlier phenology in urban habitats relying on differences in phenology and published information on fecundity and the annual number of reproductive events. Singing started earlier in urban habitats for wood pigeon and house sparrow, but not for blackbird (Table 4). Duration of the singing period, as an estimate of duration of the breeding season, was about a week longer in urban than in rural habitats. The estimated change in duration of the breeding season with latitude for all rural populations (that represent the ancestral condition) decreased significantly with increasing latitude; the partial regression coefficient of this analysis (–0.59) showed a decrease in duration of the singing period by 17.1 d between our southernmost and northernmost study sites. The estimated number of breeding cycles increased by between 3 and 20% among species, with the largest difference being in the colonial house sparrow (Table 4).

4. DISCUSSION

The main findings of this study of start and duration of the singing period in paired urban and rural populations of birds were that birds in urban populations started to sing earlier and sang for longer than conspecifics in nearby rural populations, although these effects differed among species. However, the association between urbanization and singing period was much less clear-cut than usually assumed in the literature (Gliwicz et al. 1994, Stephan 1999). Effects of urbanization on start and duration of singing period were positively related to size of cities and ecological characteristics of species. Larger city sizes, and hence larger absolute sizes of urban bird populations, amplified urbanization effects, a result consistent with the positive relationship between population size and adaptiveness also found for successful avian urban invaders (Møller 2009).

Singing periods and therefore by inference breeding seasons of urban populations were earlier and longer compared to those of ancestral rural populations of the same species just a few kilometres away. This effect was mainly due to earlier start of the singing period in urban habitats, with much less difference at the end of this period. For 3 common breeding birds in urban habitats, the increases in duration of the singing period as a surrogate of that of the breeding season in urban populations were quite large (5, 6 and 28 d) and similar to the yardstick difference of 17.1 d between our southernmost and northernmost study sites. There was considerable heterogeneity in the increase among species and populations, consistent with responses depending on local conditions during independent urban colonization events. We suggest that differences in phenology between nearby rural and urban populations may give rise to isolation by time (Hendry & Day 2005). Such effects will be further exacerbated by reductions in dispersal rate of urban populations (e.g. Stephan 1999, Møller 2009, Samaš et al. 2013b), with many urban populations having changed from being migratory or partially migratory to completely sedentary (Berthold 2001, Partecke & Gwinner 2007).

The difference in duration of the singing period between urban and rural habitats could be either phenotypic or evolutionary. Genetic differentiation between urban birds and their rural ancestors may suggest an evolutionary change (e.g. Rutkowski et al. 2005, Baratti et al. 2009, Evans et al. 2009, Björklund et al. 2010, Delaney 2014). Such differentiation is

likely due to lack of dispersal and local adjustment, either due to evolution or to plasticity of vocal behaviour (Partecke et al. 2004, 2006, Partecke & Gwinner 2007). However, the studies referred to above have very limited potential for generalization as they were based on (1) a single species in (2) a single pair composed of one urban and one rural site. Importantly, the inference in such studies is at the level of habitats (urban vs. rural, i.e. the level of analysis) and not at the level of individuals (measurement units). Therefore, it would be statistically flawed to use individuals as if they were the levels of analysis (Hurlbert 1984). In other words, no matter the number of studied individuals the relevant sample size is the number of spatial and species replicates per habitat type (see original definition and discussion by Hurlbert 1984). Generalization from such location differences, i.e. pseudoreplication, still represents the most common problem in ecology (Hurlbert 1984). Here we rigorously addressed this problem through extensive meta-replication (see also Grim et al. 2011; Møller et al. 2012, Samaš et al. 2013a) both spatially along a large European latitudinal gradient, and taxonomically, by including data for 54 bird species. Robustness of results after accounting statistically for geographic, taxonomical and phylogenetic effects strongly supported the generality of our conclusions (see Johnson 2002).

Because time since colonization affects isolation by distance (meta-analysis in Crispo & Hendry 2005), we can predict that differentiation should be particularly pronounced in species that have been urbanized for a long time. The positive relationship between difference in population density between urban and rural habitats and difference in duration of the singing period suggests that adjustment to the urban environments is a gradual process (see also Luniak et al. 1990). In contrast, a phenotypically plastic response would have predicted that changes happened relatively quickly rather than over many generations as our data suggest (see also Møller et al. 2012).

Ecological differences among species may affect timing and duration of breeding seasons because species vary in timing of peak food abundance and ability to accumulate resources necessary for initiation of reproduction (Perrins 1970, Drent 2006). Here we briefly consider three instances. (1) Winter territoriality by resident populations of robins and starlings may have arisen as a consequence of competition for limiting resources (e.g. Lack 1943). If that was the case, we should expect such species to start reproducing early in urban habitats. That was indeed what we found, with timing of the singing period

advancing in urban compared to rural populations. (2) Colonial species may often disproportionately succeed in adapting to urban environments if immigration allows many individuals to become established, thereby reducing the probability of extinction for stochastic reasons. Urban populations of colonial species had longer singing periods than rural populations (Table 3). (3) Although previous studies have suggested that resident species more often become urbanized (von Haartman 1968, Suhonen & Jokimäki 1988), we found no evidence that bird migration was associated with differences in start or duration of the singing period between urban and rural populations. Resident species had larger densities in urban than in rural populations while the opposite was the case for migratory species. This difference suggests that residents may have an advantage over migrants because they are able to occupy prime resources (e.g. nest sites) first and establish large populations. However, migrants may use residents as a cue to find suitable habitats (e.g. Mönkkönen et al. 1997), eliminating or reducing differences in advance of the singing period between residents and migrants.

The timing of vocal activity and thus the reproduction process of breeding birds is initiated in response to environmental cues. Individuals rely on weather-related factors when making decisions about the start of breeding, thereby maximizing reproductive success. Spring temperature and precipitation are known to affect timing of the breeding season (Deviche & Davies 2014). The beginning of vocal activity and the duration of the singing period were indeed related to geographic differences in weather. Both higher temperature and precipitation extended the singing period by allowing for an earlier start, without influencing the mean and final singing dates. However, we found no evidence of weather-related mechanisms underlying phenological effects of urbanization. This suggests that the timing of the singing period in urban habitats depends on additional environmental cues of an interactive nature. Previous studies have found many factors affecting the timing of reproduction when comparing urban and rural populations (see review in Deviche & Davies 2014). However, most of these studies were limited to conclusions based on just a few species. Meta-replicated experiments like the present study are more useful to address the mechanistic causes of phenological responses to urbanization. This is particularly important in the light of necessity of a unified framework for forecasting impacts of climate change on phenology, especially in changing habitats (Visser et al. 2010). Urban environments with warmer microclimates than the surround-

ing rural areas might be useful for assessment of effects of possible climate change on populations. IPCC (2013) has shown that it is principally spring temperatures that have increased in northern temperate and arctic regions as a consequence of global climate change. Such effects of increasing temperature may be particularly strong in cities (Grimm et al. 2008). Indeed, our results suggest such a difference in timing of reproduction (with singing activity as a proxy of reproductive activity) at the start of the breeding season in early spring, but not at the end during late summer. Thus, we should expect differentiation between urban and rural populations to become further exaggerated by climate change.

The mechanisms underlying the phenological differences reported here merit further comment. Successful invasion of urban areas is associated with reduced fearfulness in urban habitats as reflected by short mean and reduced variance in flight distance (Cooke 1980, Møller 2008a, 2009, 2010, Díaz et al. 2013, Møller et al. 2013). Such reduced fearfulness may allow for the faster accumulation of resources required for reproduction because urban birds waste less energy by fleeing from humans, finally resulting in increasing population trends (Díaz et al. 2015). This advantage may be enhanced by the longer growing season in urban areas (Imhoff et al. 2000), allowing for earlier start of reproduction. However, we have shown here that the start and the duration of the singing period differed between pairs of urban and rural populations. The difference in flight distance between rural and urban populations is positively correlated with time since urbanization (Møller 2008a, 2010), suggesting that species that have been urbanized for a long time differ in fear responses compared to rural populations. These differences are important because a reduction in flight initiation distance in urban habitats can be considered an optimal response to frequent encounters with humans, allowing for earlier start of reproduction in cities. In fact, bird species with long flight initiation distances for their body size have declining breeding populations in Europe, while species with short flight initiation distances tend to be thriving (Møller 2008b, 2014a). Temporal change in flight responses to humans resembles domestication because domesticated animals show reduced fear reaction and weak stress responses when approached by humans (e.g. Kohane & Parsons 1986, Wirén et al. 2009). Flight behaviour has a genetic basis and responds to artificial selection, as shown by rapid change in behaviour during domestication (Kohane & Parsons 1986, Wirén et al. 2009, Møller 2014b).

Urban areas are characterized by high resource abundance partly because of large amounts of food provided by humans (Robb et al. 2008). For example, the most abundant wintering species in Finland are able to use winter feeding sites, which provide continuous, diverse and abundant food resources for birds (Jokimäki & Suhonen 1998, Jokimäki & Kaisanlahti-Jokimäki 2003). Many studies have indicated that winter feeding has an important role in structuring the winter bird fauna (Jokimäki & Suhonen 1998, Fuller et al. 2008). We propose that high food availability might provide possibilities for earlier reproduction in urban habitats. Artificial light in urban habitats might also affect the start of singing (Kempenaers et al. 2010).

Paired designs with a consistent study area selection, study methods along a latitudinal gradient and species replication, as in our design, have never before been used in urban ecology (see also Møller et al. 2012, Díaz et al. 2013). However, our design also has some weaknesses. Because it was limited to a single year, the conclusions may not apply to other years — just as in many other ecological studies. We checked for reliability of our single-year study with data collected using the same study design and methods in Paris, France, showing comparable results in different years. We were forced, due to the inaccessibility of many private urban areas, to evaluate the start and duration of singing by birds using a single transect per habitat, although this fact is unlikely to have biased our results. Different observers collected data from each pair of sites, but as our objective was to compare urban and rural habitats (within-pairs design), the possible role of observers should not have affected the interpretation of results. Anyway, it would be clearly impossible for a single observer to collect data at a large continental scale. Finally, we used all observations of singing birds instead of using distance limits to avoid detectability effects (Voříšek et al. 2010). Detectability of species may be generally lower in urban environments (J. Reif pers. comm.), a fact that would have biased our estimates towards shorter singing periods in towns, i.e. against our hypotheses. In fact, we found strongly opposite patterns (i.e. longer urban singing periods), which suggests that detectability did not confound the conclusions of our study.

In conclusion, we have shown a heterogeneous interspecific response to urbanization in terms of timing and duration of the period of singing, and hence the duration of the breeding season. These effects were positively related to differences in population density between urban and rural habitats and size of

cities. Ecological attributes of species, such as winter territoriality and breeding sociality, explained additional differences in phenology between urban and rural populations.

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