Behavioral Ecology

Original Article

Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise

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Anthropogenic noise is a major pollutant for organisms that live in urban areas. City birds modify their songs in ways that can increase their communication potential in spite of noise. However, these changes cannot prevent song masking by the extremely loud noises to which some urban bird populations are exposed. Here, we show that birds near a major airport advance their dawn singing time, thus reducing overlap with periods of intense aircraft noise. This modification was stronger in species whose normal singing time was relatively late, those which overlapped the most with aircraft noise. Although suggestive of a causal relationship, this pattern does not allow us to tell apart the effect of aircraft noise from that of other variables that may correlate with dawn singing time. In order to control for such potentially confounding variables, we replicated the study in several airports at different latitudes in Spain and Germany. The results show that indeed the overlap of song chorus with aircraft noise was the key factor that influenced time advancement. Aircraft traffic time was the main predictor of song advancement: across Europe, those bird populations whose singing time overlapped the most with aircraft traffic were those that advanced their song timing to a higher extent. Our results exemplify how behavioral plasticity may allow the survival of avian populations in areas of high noise pollution. However, such an adaptation likely involves departing from optimal singing times, leading to higher energetic costs and amplifying between-species differences in competitive ability and resilience.

Key words: **acoustic pollution, bird song, down chorus, noise, urbanization.**

INTRODUCTION

Birds rely on vocal communication to perform many vital functions such as attracting mates, defending territories, or warning conspecifics against predators (Bradbury and Vehrencamp 1998; Catchpole and Slater 2008). One of the advantages of vocal communication is the possibility of encoding individual and species information in signals and transmitting them over relatively large distances. In the case of songbirds (*Passeriformes*), a complex neural system allows song learning, and specific neuromuscular innovations for song production permit fine modifications of pitch, intensity, and song content (Zeigler and Marler 2008), resulting in one of the most complex and subtle animal languages that we know of (see for instance: Fortune et al. 2011; Perez et al. 2012).

One important constraint for acoustic communication is noise, which may mask the signals, or parts of them, thus hampering

information transfer. Noise originates from various sources, both natural and anthropic, and depending on its amplitude, it can limit or preclude vocal communication. It has been shown in many species that birds rely on a number of adaptations to reduce the impact of noise (Gil and Brumm 2014). Some of these include increases in amplitude that augment the effective distance over which songs can be perceived (Brumm 2004; Zollinger and Brumm 2011; Lowry et al. 2012), and modifications of song frequency that reduce masking with noise (Slabbekoorn and Peet 2003; Ríos-Chelén et al. 2012), although it has been recently shown that increases in amplitude are far more effective than pitch modifications and that the latter strategy might be an epiphenomenon of amplitude changes (Nemeth and Brumm 2010; Nemeth et al. 2013). An additional strategy is to modify the content of the song in noisy situations, meeting expectations of signal theory that predict higher signal redundancy when perception is hampered (Brumm and Slater 2006). However, apart from direct song modifications, some bird species have been shown to modify song activity schedules to reduce overlap with periods of high noise. For instance,

European robins *Erithacus rubecula* are more likely to sing at night in noisy than in quiet cities, thus using a time when city noise levels are lower (Fuller et al. 2007). Similarly, the start of the dawn chorus in European blackbirds *Turdus merula* was found to be dependent on traffic noise and light levels (Nordt and Klenke 2013).

Airports can provide an interesting contrast to these urban phenomena because of 2 main characteristics: first, noise periods are highly predictable, with a sudden peak of flying starting typically right before dawn; second, aircraft noise levels are so loud that song modifications of pitch or amplitude cannot improve perception by the intended receivers (frequent flights reaching >110 dB near airports: Smith 1989). We hypothesized that birds living near airports would modify their circadian singing patterns to avoid periods of high levels of aircraft traffic. Most birds in the Northern Hemisphere show their highest period of vocal activity within the first 2 h before dawn (Staicer et al. 1996), and each species tends to have a specific time to start singing (Thomas et al. 2002). Because of civil regulations and industry logistics, flight traffic in Europe typically starts around 6.00 AM and quickly increases to very high levels that last during the rest of the morning. Given this coincidence in time, we predicted that birds would advance their dawn chorus near airports to reduce their overlap with aircraft activity.

We conducted a first study near Madrid airport to test this hypothesis. The following year we replicated this study in several more airports in Europe differing in latitude. The rationale of this second study was to tease apart the effect of dawn time and that of airport noise. Whereas human standard time is not tied to astronomic timing, bird dawn chorus closely tracks sunrise (Staicer et al. 1996), and thus, the overlap between peaks of aircraft noise and dawn chorus varies at different latitudes. We predicted that song advancement should be greater at latitudes in which meteorological dawn and standard human times are closest to each other (Warren et al. 2006) and that airport-linked advancement in dawn chorus timing should be related to human standard time and not to astronomic dawn time.

MATERIALS AND METHODS

Study areas

This article reports the results of 2 different pieces of work. The first study was conducted near Madrid airport in 2011, and the second was expanded to 5 different airports in 2012 (see Supplementary Figure S1 for a comparison of number of flights in the different airports). In the case of the Madrid airport study, we took advantage of a strip of continuous riverine habitat that runs next to Madrid international airport (Barajas Airport, IATA code: MAD), ranked as the 19th busiest airport in the world with nearly 50 million passengers a year (IATA 2013). This allowed us to obtain homogenous stretches of similar habitat at different distances from the airport, exposed to dramatically different noise regimes (see noise contours in Figure 1). We chose 3 different sites, located at 3 distances from the airport and subject to very different noise levels (Lden data provided by the airport noise map available at: www.aena-aeropuertos.es): control zone at 50–55 db(A), intermediate zone at 65–70 dB(A), and airport zone at 70–75 db(A). "Lden" is a standard average measure of sound pollution in human environments, corresponding to the average sound level over a 24-h period, with a penalty of 5 dB added for the evening hours of 19:00 to 22:00 and a penalty of 10 dB added for the nighttime hours of 22:00 to 07:00 (Cowan 1993). The mean noise level for the airport zone is within levels that have been shown to lead to sound masking

in the case of bird perception (corresponding to "Zone 3" following a recent study: Dooling and Blumenrath 2013). Note that Lden data are daily averaged means, but that aircraft flying overhead in this area typically lead to peaks of >110 dB (authors' own observations). It is important to stress that the airport zone we studied is situated outside the off-limits area of the airport, at the very end of the runway, and in a rural area that is not affected by road traffic or lights related to the airport.

In the case of the multiairport study in 2012, we selected 5 airports differing in latitude (Barcelona, Madrid, Valencia and Malaga in Spain, and Berlin Tegel in Germany; Supplementary Table S1). Areas were chosen by overlaying noise contours (in Lden) taken from airport noise maps (available at www.aena-aeropuertos.es and www.stadtentwicklung.berlin.de), over Google Earth images (at 1:3000 scale) in order to detect suitable areas that were differentially affected by aircraft noise. We confirmed the suitability of the areas by visiting the sites, discarding those that were exposed to other sources of acoustic (nearby busy roads or trains) or light pollution. We favored woodland areas of comparable vegetation structure. In this study, we sampled 2 extreme noise areas per site (Lden: <55 [control] and >70 dB(A) [airport]). Geographic coordinates of each area are given in Supplementary Table S1.

Song activity monitoring

We used automatic sound recorders: Song Meter™ (models SM1 and SM2 from Wildlife Acoustics), programmed to record from 3 h before dawn until 2 h after dawn in 10-min intervals alternating with 10 min of inactivity. Recorders were set in custom-made harnesses and hung from branches at a height of 1–3 m with the help of poles. Recordings (wav files, 48 kHz, 16 bits) were transferred from memory cards to a hard disk by means of a laptop.

Within each area, we selected sampling points separated by a minimum of 100 m from each other. In the 2011 Madrid airport study, we recorded daily from 10 May to 7 June, changing sampling points every 3–5 days (sampling point was added as a random factor in the analyses). In the 2012 multiairport study, we sampled at different points every day and recorded simultaneously in the 2 areas during May–June 2012 (recording days: 4 [Madrid], 4 [Barcelona], 3 [Malaga], 6 [Berlin], and 3 [Valencia]).

Recordings were monitored in the lab with Sennheiser HD-280 headphones. Monitoring work was limited to 2–3 h per day to avoid fatigue and identification oversights. Doubtful songs were shared and discussed between different observers and song libraries consulted if needed (e.g., www.xenocanto.org). In each recording, we set dawn time as 0, and song detections were codified as species-specific presence/absence (0–1) within each time interval (negative time meaning minutes before dawn). First-song time was defined as the midpoint of the earliest time interval in which a species song was detected in a given day (calls were not considered in the analysis). Song period was defined as the number of 10-min intervals in which a given species was heard singing, multiplied by 2 to account for sampling effort. Note that our data for singing period are a rough approximation of singing activity because we did not measure song rates, and detections are only based on presence/absence data in intervals of 10 min.

Avian community composition and vegetation comparison

We transformed species-specific occurrence data from the Madrid 2011 recordings into daily presence/absence data matrixes from which qualitative point counts were obtained (Blondel 1977). To compare vegetation between sites in the Madrid 2011 study, we
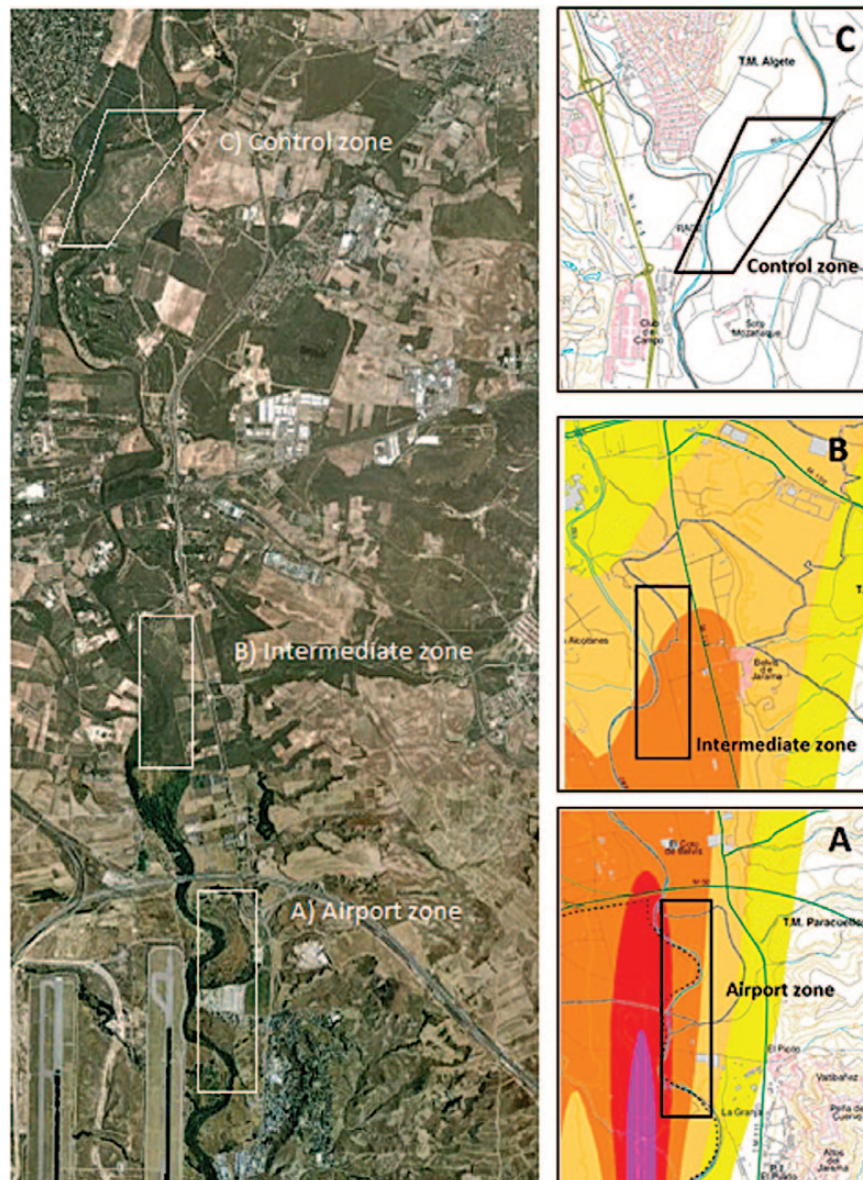
Figure 1

Location of the 3 areas of the Madrid airport study from a Google Earth image (left) and extracts from the Barajas airport noise map (right) indicating the 3 areas used in the study (www.aena-aeropuertos.es): (A) airport zone, (B) intermediate zone, and (C) control zone. Colors represent intervals of noise levels measured following the Lday international protocol—purple: >75 dB(A), red: 70–75 dB(A), orange: 65–70 dB(A), light brown: 60–65 dB(A), yellow: 55–60 dB(A), and white: <55 dB(A).

used 1:3000 Google Earth images and overlaid a grid of squares of 3.6 cm per side that covered the extension of the 3 zones. In each square, we estimated vegetation cover in situ (in a scale 1–5) for the following 2 categories: arboreal cover (main species: *Ulmus minor*, *Fraxinus angustifolia*, and *Populus alba*) and shrub-herbaceous cover (*Tamarix gallica*, *Phragmites australis*, *Scirpus lacustris*, *Typha domiguensis*, *Rubus ulmifolius*, and *Silybum marianum*).

Light pollution measurements

We measured sky brightness (mag/arcseg²) in the 3 sites used in the 2011 Madrid study, which is an estimate of sky darkness used by astronomers to characterize light polluted sites, and has been used before to assess biologically relevant urban light pollution levels (Kyba et al. 2011; Davies et al. 2013). Measures were taken for 1 month, between 3 h before and 2 h after dawn, at intervals of 10 min. We used 3 Sky Quality Meter LU-DL meters (Unihedron, Grimsby, and Canada), 1 per zone, that were moved every week to a different point. Meters were placed 3 m above ground in the gallery forest, at 2–4 m from the river bed. We specifically tested differences in night light pollution between sites (between 180 and 100 min before dawn, which is the key time when advancement was detected), using a general linear mixed model (GLMM) in which recording point was declared as random factor within areas.

Bird eye size

Some previous studies have found that relative eye size is a good predictor of singing time, probably because larger eyes can allow birds to become active at lower light thresholds (Thomas et al. 2002; Berg

et al. 2006), and thus, we controlled for this effect in the analysis of first-song time. Published eye size data (Ritland 1982; Thomas et al. 2002; Møller and Erritzøe 2010) did not include all the species that we studied; thus, we used a recently developed method for calculating eye size from bird pictures (Martínez-Ortega et al. 2014). We chose pictures taken with a lateral perspective with the bird in the hand, which were processed using image software (ImageJ, version 1.46r, Wayne Rasband, National Institutes of Health, public domain). As size reference standard, we used mean beak height obtained from museum skins available at the Museo Nacional de Ciencias Naturales (Madrid) (mean: 4.5 individuals per species, standard deviation [SD] = 0.60; range: 3–5, repeatability: $r = 0.98$; $F_{21,77} = 254.4$, $P < 0.001$). The beak reference point for measurements was chosen to fit the morphology of each species. In species with exposed narines, we measured beak height at the narine distal extremity. In the case of species that had concealed narines (e.g., great tit, *Parus major*), we used the beginning of feathers over the beak as reference point. We used pictures in which the bird head was shown sideways, mostly from an online collection (www.javierblasco.arrakis.es), but also from other sources (e.g., www.tarsiger.com and ibc.lynxeds.com). From each picture, we estimated exposed eye area by using the "polygon" tool from the package ImageJ® after setting the relevant scale with reference to mean beak height (obtained from skins). An average of 3.5 pictures was examined per species (SD = 0.85, range = 2–6; repeatability = 0.95; $F_{21,55} = 53.6$, $P < 0.001$). Our estimates were strongly correlated with previous estimates (Supplementary Figure S3) regressions of eye size (controlling for body size) on eye volume (Møller and Erritzøe 2010): $F_{1,14} = 23.8$, $P < 0.001$, $r^2 = 0.60$; on external eye width (Thomas et al. 2002): $F_{1,15} = 110.9$, $P < 0.001$, $r^2 = 0.87$; and transverse eye diameter (Ritland 1982): $F_{1,10} = 20.02$, $P < 0.001$, $r^2 = 0.63$. Because eye size is strongly dependent on body mass, and adding both body mass and eye size in the model leads to high collinearity (variance inflation factor > 12 in models described below), we worked with eye size residuals as obtained from the linear regression of eye area on body mass ($F_{1,19} = 88.76$, $P < 0.001$, $r^2 = 0.81$).

Statistics

In the 2011 Madrid study, we selected species that had been detected at least 7 times per zone, which led to a sample size of 10 species (Supplementary Table S2), after dropping the following species with fewer detections: *Acrocephalus scirpaceus*, *Turdus philomelos*, and *P. major*. Data were expressed as minutes with respect to civil dawn (also called civil twilight, corresponding to the moment when the sun is 6° below the horizon). We ran global GLMMs in Proc Mixed (SAS) for first song at dawn and singing period, including date and minimum temperature as covariates and species and sampling point as random factors. These models provided us with a general test of between-zone heterogeneity, controlling for multiple testing (species as random effect). In order to obtain species-specific estimates, we ran similar models, but in this case species identity was declared a fixed factor, together with its interactions with zone and temperature. We chose models with minimum Akaike information criterion (AIC) values and used least square means from these models for interspecific tests. In the 2012 multiairport study, we applied a similar procedure but, given the reduced sampling, we relaxed the criteria and accepted bird species that had been detected at least 3 days per zone in the 2 zones of each airport.

Among-species comparisons were done by contrasting standardized effect sizes, using Hedges' g statistic (Ellis 2010) based on least square means from the models. Analyses were performed using a general linear model (gls) using the package ape in R (Paradis et al. 2004; R Foundation for Statistical Computing 2013) and controlling for (molecular) phylogeny. A consensus phylogenetic tree was obtained by majority rules from mitochondrial data collated by Jetz et al. (2012) and available at http://birdtree.org (Supplementary Figures S4 and S5). Trees were ultraparameterized before use. We compared Brownian random-walk models with alternative Ornstein–Uhlenbeck modes of evolution, and in all cases, the best fit was achieved with the former.

RESULTS

Madrid airport study

The 3 areas selected at different distances from the airport and subject to large noise differences did not differ in avian community composition (Supplementary Table S2), with identical absolute richness (13 species in the 3 zones) and similar mean richness per point count (Anova, $F_{2,84} = 0.53$, $P = 0.58$). The probability of detection per species was very similar in all species (Supplementary Table S2), with the exception of the great tit (*P. major*), which showed higher detection in the quietest area. However, because the lowest detection for this species was at the intermediate zone, it is unlikely that differences in noise alone are responsible for these differences in detectability.

The 3 areas covered a continuous riverine habitat (Figure 1), and indeed, Kruskall–Wallis tests showed no differences between areas in either arboreal cover ($\chi^2 = 2. 36$, degrees of freedom [df] = 2, $P = 0.31$) or shrub-herbaceous cover ($\chi^2 = 0.41$, df = 2, $P = 0.82$). Although the 3 areas were well outside road and airport lighting, we controlled for possible differences in light pollution. Our analysis of a monthlong series of recordings (Supplementary Table S3) showed that light pollution levels were homogenous between the 3 zones: light increases smoothly and homogenously in all zones from night to daytime (Supplementary Figure S2).

The global GLMM for time of first song (minutes with respect to civil dawn), for the 10 commoner bird species found in all areas, and including date and minimum temperature as covariates, showed strong effects of zone, with a significant effect of species as random factor (Table 1). Globally, the time of first song decreased (occurred earlier) as we approached the airport. An inspection of the species-specific means obtained from a model in which species was declared as fixed factor (Supplementary Table S4) reveals that all species sang earlier at the airport end of the noise gradient (Figure 2). Significant interactions of species identity with zone, date, and temperature reflect the fact that species differed in how much they shift their singing time in response to these variables.

On average, the difference in the time of first song between the airport and the control zone was 23.8 min (SD = 10.76). Although all species shifted their timing in the same direction, the extent of this advance varied substantially (Figure 2). Because aircraft

Table 1

Results of a GLMM on first-song time at the Madrid airport, considering species and recording point as random factors

Term in model	F (or $\mathcal{Z}$)	df	P
Zone	30.43	2,20.4	<0.001
Date	6.63	1,22.4	0.017
Temperature	3.89	1,109	0.051
Sampling point (random)	1.31	Not applicable	0.096
Species (random)	2.11	Not applicable	0.017
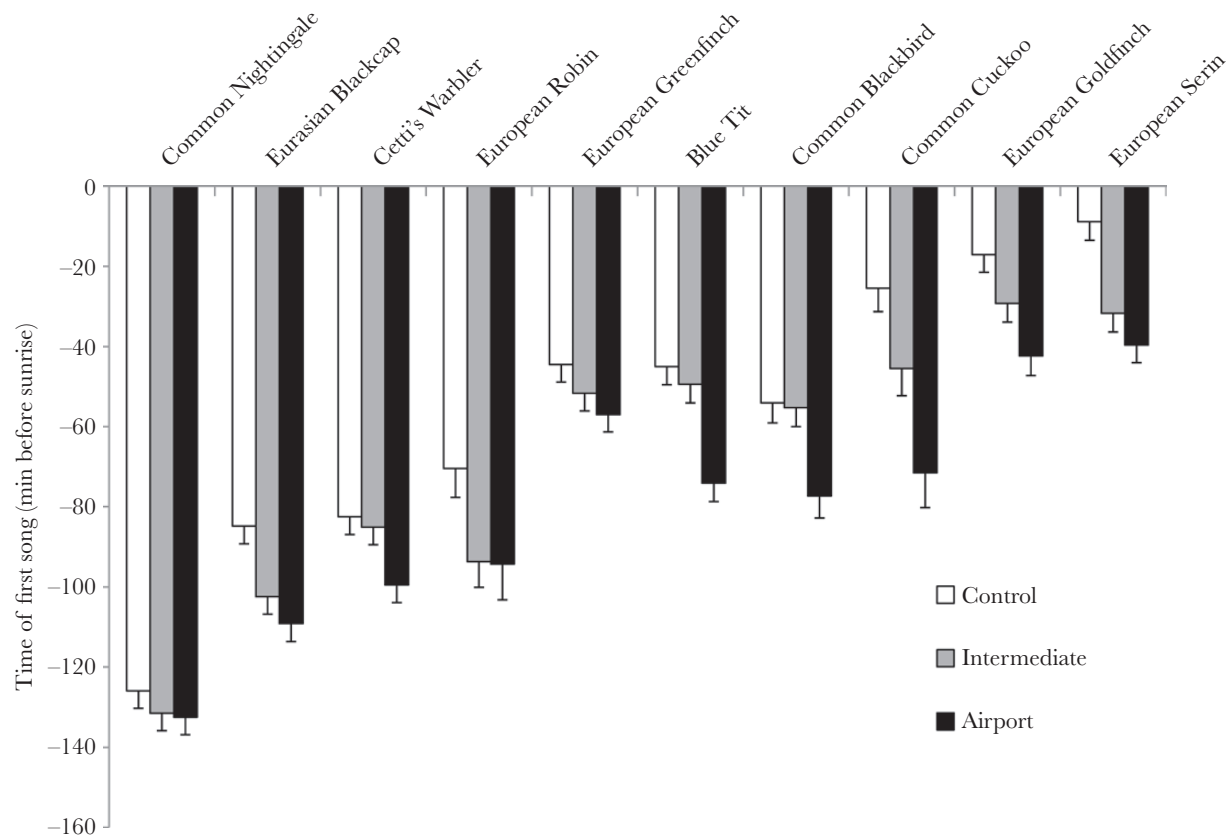
Figure 2

Least square means (−1 SE) for first-song timing of the 10 bird species at Madrid airport at the 3 different zones differing in noise levels. Species are ordered with respect to absolute timing in the control zone. Scientific names for these species are as follows: European goldfinch (*Carduelis carduelis*), European greenfinch (*Carduelis chloris*), Cetti's warbler (*Cettia cetti*), common cuckoo (*Cuculus canorus*), European robin (*Erithacus rubecula*), common nightingale (*Luscinia megarhynchos*), Blue Tit (*Parus caeruleus*), European serin (*Serinus serinus*), Eurasian blackcap (*Sylvia atricapilla*), and common blackbird (*Turdus merula*).

traffic starts at 6.00 AM at Madrid airport, peaking an hour or so later (Supplementary Figure S1), it is to be expected that those species that normally sing relatively late should show a greater shift to avoid overlap than those that sing much earlier than dawn. We tested this prediction using species-specific standardized effect sizes: Hedges' *g* statistic on the difference of timing between airport versus control area (least square means obtained from a generalized linear model (GLM) with species as fixed factor: Supplementary Table S4) and considering body mass and relative eye size in the model. Using a phylogenetically informed model (Supplementary Figure S4), we found that birds that presented a greater time shift near the airport are those that normally sing the latest and have relatively larger eyes (Table 2 and Figure 3).

Does this advance in time lead to an increase in song activity effort throughout the day? The global GLMM for song period (Table 3) shows an overall difference between sites, with very slight longer periods near the airport. When we examined interspecific differences in song period using species-specific standardized effect sizes: Hedges' *g* statistic on the difference of song period between airport versus control area (least square means obtained from a GLM with species as fixed factor: Supplementary Table S5), considering body mass and relative eye size in the model and controlling for phylogeny, we found that the effect was stronger for late-singing and relatively large-eyed species (Table 4). Inspection of Figure 4, however, suggests that this pattern was strongly dependent on 2 late-singing species (*Serinus serinus* and *Cuculus canorus*) and should be regarded with caution.

Table 2

Results from a phylogenetic general linear model (gls command in package ape in R) on the magnitude of song time advance by the different species in the Madrid airport study, in relation to first-song time at the control zone, relative eye size, and body mass

Term in model	Estimate	SE	*t*	*P*
Time in control area	0.018	0.002	11.22	<0.001
Body mass (log)	0.17	0.183	0.97	0.367
Residual eye width (log)	7.672	1.365	5.61	<0.01

Lambda estimated at 1.59 assuming random Brownian evolution. SE, standard error.

Multiairport study

We obtained data on first song for 39 different populations belonging to 21 species (mean [SD]: 2.58 [0.98] populations per species) and computed effect sizes of time advancement (airport vs. control) using Hedges' *g* to standardize effect sizes. We tested whether this time advancement was dependent on how close was the species-specific dawn singing time (as measured at the control zone) to human standard time (arbitrarily zeroed at 6:00 AM) or whether time advancement was dependent on astronomic dawn time. For brevity, we will, respectively, use the terms "proximity to rush hour" and "proximity to dawn" to refer to these 2 estimates.

Here, we encounter the statistical complication of using several populations per species, which can lead to pseudoreplication if data points are not independent. To test this latter assumption, we
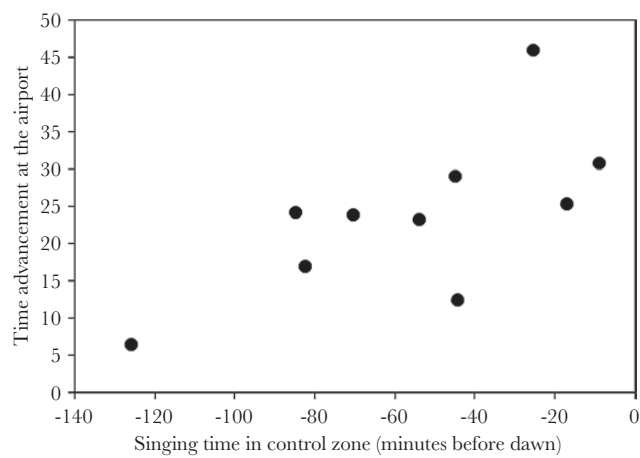
Figure 3

Species-specific advance in song timing at the airport zone in the Madrid study, with respect to timing in the control zone. Data shown are estimates as obtained from least squares means; note that the statistical analysis is based on effect sizes controlling for species-specific variation.

Table 3

Results of a GLMM on song period at the Madrid airport, considering species and recording point as random factors

Term in model	F (or $\mathcal{Z}$)	df	P
Zone	3.68	2,21.8	0.042
Date	11.26	1,23.6	0.002
Temperature	2.92	1,106	0.091
Sampling point (random)	1.20	Not applicable	0.114
Species (random)	2.12	Not applicable	0.017

Table 4

Results from a phylogenetic general linear model (gls command in package ape in R) on the magnitude of increase in song time period of the different species in the Madrid airport study (difference between song period near the airport and in the control area), with respect to first-song time at the control zone and relative eye size

Term in model	Estimate	SE	t	P
Time in control area	0.022	0.006	3.74	0.009
Body mass (log)	0.38	0.43	0.87	0.414
Residual eye width (log)	10.60	3.53	3.00	0.02

Lambda estimated at −1.52 assuming random Brownian evolution. SE, standard error.

analyzed the relationship between time advancement and proximity to dawn with 2 types of model: a linear model and a mixed model that included species as random factor (either as intercept or intercept plus slope). Restricted maximum-likelihood comparison of models showed that the better fit was obtained by the linear model and that the contribution of species as random factor was negligible (data not shown). That differences between species were smaller than differences within species suggests that time advancement is not a species-specific trait, but rather varies between populations, and that it is not necessary to correct for phylogenetic similarity. We thus used linear models to analyze time advancement as dependent on singing time with respect to dawn or to rush hour. As in the case of the Madrid data set, we included in the model body mass and residual eye size. Because dawn time and rush hour are highly
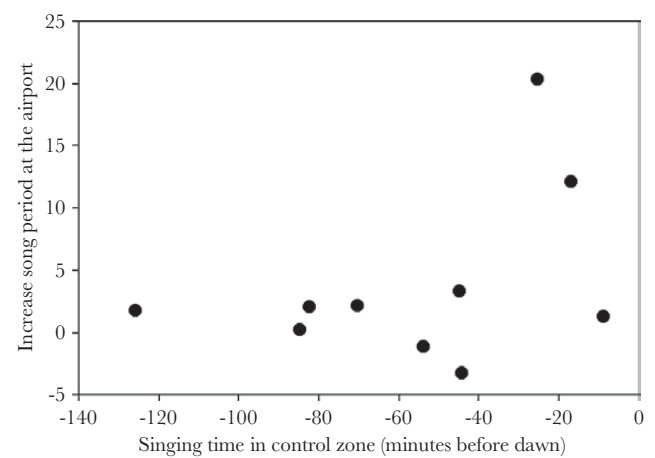
Figure 4

Species-specific increase in song period at the airport zone in the Madrid study, with respect to timing in the control zone. Data shown are estimates as obtained from least squares means; note that the statistical analysis is based on effect sizes controlling for species-specific variation.

correlated, we compared models with either predictor as fixed effect, using a maximum-likelihood model-averaging approach to select the best models. In the case of proximity to rush hour, all selected models conserved this predictor, with various combinations of residual eye size and body mass (Table 5 and Figure 5), confirming that proximity to the aircraft noise timing was the main driver behind the shift. By contrast, models with dawn time as predictor were not more likely than a null model, suggesting that none of the terms was a useful predictor of timing advancement (Table 6).

In order to test the robustness of the effect, and to control for the interspecific phylogenetic signal, we bootstrapped phylogenetically informed models ($N = 1000$) so that in each resample, only one population per species was considered, thus using a reduced number of populations. This allowed us to run GLMs with phylogenetic correction (phylogeny shown in Supplementary Figure S5). The mean effect for proximity to rush hour showed a similar pattern to that reported earlier (mean F [SD]: 4.68 [4.52]; estimate [SD] = 0.004 [0.001], df = 19, $P = 0.043$). Although there is a large variance in the strength of the association due to random sampling, the mean result and the positive estimate confirm the pattern found in the previous model including all populations.

DISCUSSION

To summarize, across a wide range of latitudes, bird populations advanced their morning song chorus in relation to the degree of overlap between dawn and civil time. In Southern populations, where standard time is closer to meteorological dawn in spring, bird populations living close to airports advanced their song to a larger extent than in Northern populations, where dawn occurs considerably earlier than human standard time. In other words, those species and populations who normally sing closer to the time when aircraft traffic peaks responded to aircraft noise pollution with a larger advance in their dawn chorus (Figure 2).

The pattern that we found shows a strong contrast with the effect of light pollution (Kempenaers et al. 2010), which has been found to produce larger time advances in species that sing earliest in the day. This difference suggests that the modification that we have detected is not due to circadian constraints, but likely reflects

Table 5

Maximum likelihood comparison of models for time advancement (airport vs. control) using standardized effect differences (Hedges' *g*) and using as main predictor proximity between singing time and human standard time (rush hour) in the multiairport study

Terms in model	df	Log likelihood	AICc	Delta	Weight
Models with highest AICc (delta < 4) using proximity to rush hour					
Logmass + rush	4	−43.97	97.11	0	0.41
Rush	3	−43.35	97.39	0.28	0.36
Logmass + reseye + rush	5	−43.93	99.68	2.57	0.11
Reseye + rush	4	−45.30	99.77	2.66	0.11

Term	Estimate	SE	Adjusted SE	*z* value	*P*(>*z*)
Model-averaged coefficients (delta < 4) using proximity to rush hour					
Intercept	0.253	0.539	0.547	0.276	0.782
Rush	0.007	0.002	0.002	2.878	0.004
Reseye	0.861	2.994	3.099	0.278	0.781
Logmass	0.616	0.378	0.391	1.566	0.117

We also included in the model body mass and residual eye size. Codes for terms are rush: proximity to rush hour, reseye: residual of eye width (log) of logmass, and logmass: body mass (log). SE, standard error.
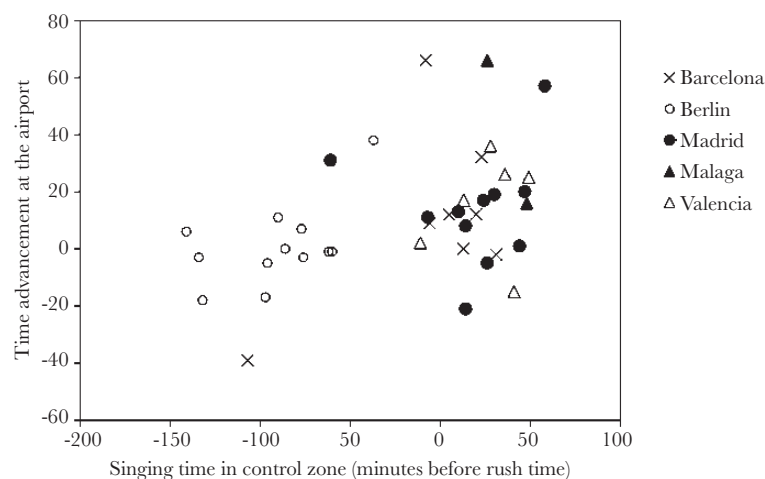
Figure 5

Species-specific advance in song timing at the airport zone in the multiairport study, with respect to rush time in the control zone. Data shown are estimates as obtained from least squares means; note that the statistical analysis is based on effect sizes controlling for species-specific variation, thus significant trends are not necessarily depicted in the plot.

Table 6

Maximum likelihood comparison of models for time advancement (airport vs. control) using standardized effect differences (Hedges' *g*) and using as main predictor proximity between singing time and dawn time in the multiairport study

Terms in model	df	logLik	AICc	Delta	Weight
Models with highest AICc (delta < 4) using proximity to dawn time					
Null	2	−49.35	103.04	0	0.34
Logmass	3	−48.86	104.41	1.37	0.17
Reseye	3	−48.94	104.57	1.53	0.16
Dawn	3	−49.24	105.17	2.13	0.12
Reseye + logmass	4	−48.32	105.81	2.77	0.08
Dawn + logmass	4	−48.51	106.2	3.16	0.07

Term	Estimate	SE	Adjusted SE	*z* value	*P*(>*z*)
Model-averaged coefficients (delta < 4) using proximity to dawn time					
Intercept	0.386	0.428	0.437	0.811	0.417
Logmass	0.404	0.417	0.43	1.005	0.315
Reseye	−2.742	2.955	3.05	0.897	0.370
Dawn	0.002	0.004	0.004	0.563	0.572

We also included in the model body mass and eye size. Codes for terms are rush: proximity to rush hour, reseye: residual of eye width (log) on logmass, and logmass: body mass (log).

adaptive change due to differential pressure of human noise at different times of the day.

What does this behavioral change imply for birds living near airports? Dawn song takes place, normally, within a span of time in which the birds are physiologically prepared to commence their activities, slightly before the time when they can visually navigate (McNamara et al. 1987). Depending on species and season, song serves 1 or 2 major functions: to advertise territorial occupancy to potential intruders and to signal reproductive readiness to potential partners. Thus, it is to be expected that a bird that advances its singing time will be increasing its vigil and metabolic rate (Bryant and Tatner 1991; Cuthill et al. 2000), without increasing energy intake. The extent to which this affects different species must vary not only with the magnitude of the change but also with the ability of the species to adjust their foraging behavior to the new timing. Our data only show a slight increase in time spent singing near the airport in 2 out of the 10 species, suggesting that these costs imposed by song-noise overlap may not lead to longer singing periods, although it is also possible that our analysis for this particular measurement is not sufficiently fine-grained to detect differences. An additional consideration is that during the breeding season, energetic and foraging costs may impact males and females alike because females need to attend male songs to select partner and adjust their reproductive effort (Halfwerk et al. 2011).

Other potential consequence is an increased singing overlap with other species. The presence of other species is a source of noise in itself that may have shaped the structure of the multispecies dawn chorus to reduce masking (Planque and Slabbekoorn 2008). Indeed, the fact that the trend in Figure 3 has a slope >0 indicates that there is a greater degree of chorus overlap between species near the airport zone than those in the control zone. Again, during the breeding season, females would also experience this cost of higher masking because they need to discriminate males by their song. In addition, singing birds advertise their location to potential predators (Schmidt and Belinsky 2013), and it could be argued that the longer birds sing in darkness, the more vulnerable they may become to nocturnal predators. This may disproportionately disadvantage late-singing species because they advance more the initiation of their chorus and have a poorer vision in dark conditions (Thomas et al. 2002).

As for the mechanisms, it remains to be studied whether modifications in the production of the main circadian hormone, melatonin, are responsible for this shift in song (Wang et al. 2012). Recent research suggests that reduced melatonin release in city birds may be linked to early start of the circadian cycle (Dominoni et al. 2013). However, melatonin also affects numerous immune processes (Rodríguez et al. 2001), and changes in the circadian pattern may affect the immune capacity, and thus, individual bird fitness at populations affected by early-morning aircraft noise peaks.

It is tempting to suggest that the observed pattern is an adaptation brought about locally by natural selection operating on increasingly earlier birds, rather than the effect of behavioral plasticity (Bermúdez-Cuamatzin et al. 2011; Slabbekoorn 2013; Partecke 2014). This is because our data show that birds change their behavior in anticipation of the event (sharp increase in aircraft noise), and it is uncertain which external cues could systematically precede air traffic morning peak and be available to birds. So, it seems more likely that selection has operated on natural variation of chorus initiation in these populations although experimental work should be conducted to answer this question. A controlled experiment using aviaries could be conducted to determine whether acoustic exposure to aircraft traffic noise regimes results in an advancement of song routines. A previous study has shown that birds that are waken up earlier do start to sing earlier (Arroyo-Solis et al. 2013), but our results suggest that birds may anticipate the occurrence of aircraft noise, or else be selected to sing earlier.

We found that the magnitude of the chorus advancement to escape peak aircraft noise varied between species, suggesting differential levels of disturbance and/or resilience between species. To the extent that singing time might be related to trophic specialization (Thomas et al. 2002), our results suggest that different bird guilds would be differently affected by aircraft noise pollution, leading to a poor balance of population services provided by bird populations (Francis et al. 2012) in localities affected by aircraft pollution. For instance, we expect that seed-eating species, which sing latest in the day, should suffer a higher cost than other guilds. Additionally, those species with sufficiently plastic behavior to escape noise masking without sacrificing much in ecological terms are likely to thrive best in the vicinity of busy airports. Inevitably, only a fraction of the species native to a particular area would fit the bill, and the resulting bird community would be both poorer and impact the ecosystem in different ways than the original one, even if the conservation efforts lead to spare as much natural habitat as possible around busy airports.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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