ORIGINAL ARTICLE

Lack of consistent responses to aircraft noise in dawn song timing of bird populations near tropical airports

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Abstract

Birds living near airports can reduce the noise interference by advancing their dawn chorus timing and avoiding the start of airport operations. Data supporting this finding come from temperate areas, but little is known from tropical environments, where seasonal variation is lower and biodiversity is higher. Here, we investigated whether 15 tropical bird species are able to advance their dawn song and avoid aircraft noise interference. We sampled dawn song in three airports and three control sites in Brazil, using automated recording units. We found that dawn song times were not globally affected by the exposure to airport noise. Instead, changes were highly variable and species-specific, as dawn song onset was significantly advanced in two and delayed in four species. This large variation in responses was surprising given patterns found in previous studies. Indeed, this is the first time that a significant delay is reported for bird's dawn song. We explored whether between-species differences in this response could be explained by additional variables (song frequency, degree of urbanity, and noise release), but none of them explained the direction or the strength of the changes. We suggest that earlier airport activity and shorter variations in day length and in twilight duration of tropical areas may be restricting birds' ability to change dawn song timing. Further studies should consider these differences and analyze to what extent populational declines in noisy areas and the resultant reduced competition for acoustic space may be affecting the changes in dawn chorus onset time.

Significance statement

Birds have been shown to advance the timing of their song at dawn to avoid airport noise in Europe. However, we did not find a similar pattern in the birds near three Brazilian airport-affected sites, where the tropical environment can be a key factor (higher biodiversity and lower seasonal variation). We found that of the 15 studied species, only two followed this pattern, 9 species showed no changes in their timing, and 4 species showed the opposite trend, delaying their dawn song in an apparently non-adaptive manner. Neither differences in the birds' song frequencies and degree of urbanity nor the noise release could account for delays in dawn song. We suggest that the birds' ability to change their song timing may be limited by shorter seasonal light variations in tropical areas and by earlier airport activity in studied sites.

Keywords Avian · ARUs · Brazil · Dawn chorus · Passeriformes · PAM

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Introduction

Wild animals are frequently subjected to anthropogenic changes that can potentially affect their behavior and fitness. In the case of birds, anthropogenic noise interferes with acoustic communication (Brumm and Zollinger 2013), which is used in various life-history contexts, from mate attraction and territory defense to parent-offspring communication (Catchpole and Slater 2008). Trying to deal with these interferences, birds modify their vocal behavior, making changes in their vocal characteristics (i.e., frequency and amplitude), and even vocalizing at unusual times of the day and night (Brumm 2004; Partecke et al. 2004; Brumm and Slabbekoorn 2005; Fuller et al. 2007; Kempenaers et al. 2010; Nemeth and Brumm 2010; Schuster et al. 2012; Nordt and Klenke 2013; Sierro et al. 2017). Many of these modifications have been interpreted as adaptive adjustments that benefit birds producing these signals (Schuster et al. 2012; Gil and Brumm 2014), the release from noise-masking being the clearest benefit (Nemeth and Brumm 2010). Behavioral plasticity offers the possibility of fast and dynamic changes in response to the fluctuations in environmental factors (Wong and Candolin 2015). However, it is not clear to what extent these changes are due to phenotypic plasticity (short term and learned) or are also the consequences of natural selection (long term and genetic) (Partecke 2014).

Anthropogenic noise and light pollution are two of the most obvious urban challenges that may contribute to altered singing behavior in birds. The independent contributions of these two elements, although difficult to tease apart (Bergen and Abs 1997; Nordt and Klenke 2013; Dominoni et al. 2020), have been shown to modify acoustic signals in urban environments (Fuller et al. 2007; Nemeth and Brumm 2010; Nordt and Klenke 2013). Noise imposes an important constraint in communication by limiting the spectral acoustic space of signaling birds and leading to a reduced probability that the signal will reach its targeted receiver (Wiley 2013). In the case of light pollution, increased light levels may induce abnormal nocturnal activity, impacting circadian sleep cycles and affecting behavior and mating patterns (Kempenaers et al. 2010).

The dawn chorus is a peak of bird vocal activity that starts approximately 30 min before twilight and is intensified during the breeding season (Catchpole and Slater 2008). In this period, many bird species take part in the chorus, although they show species-specific timings for their first song of the day (Staicer et al. 1996; Gil and Llusia 2020). Both individual singing rates and number of species singing reach a maximum in this period of the morning and then typically decrease as light intensity further increases. At this point, many singing birds initiate other daily activities, such as foraging, that interfere with intense singing and reduce singing rate (Hutchinson 2002; Burt and Vehrencamp 2005). The songs at dawn are often more intense, versatile, and complex than later during

the day, and some species have specific songs that are only produced at this time (Staicer et al. 1996; Leger 2005). During the rest of the day, these species produce either different songs (e.g., *Elaenia chiriquensis*) or very simple calls (e.g., *Coryphospingus cucullatus* and *Neothraupis fasciata*) (Staicer et al. 1996).

Only few studies have explored dawn choruses in the Neotropical region, where the number of participating species can be a challenge for acoustic recognition. This complexity is increased by the addition of suboscine species that do not occur in temperate areas (Tobias et al. 2012), and that have been shown to start singing earlier than oscine species (Ecuador; Berg et al. 2006). Apart from what is known from temperate regions, the less pronounced seasonal variation in time of civil twilight (± 1 h in the tropical vs. ± 3 h in temperate regions; Fig. 1a), in day length (± 1.9 h in tropical vs. ± 5.8 h in temperate regions; Fig. 1b), and in duration of civil twilight (50–60 min in tropical vs. 60–90 min in temperate regions; Fig. 1c) might be key factor structuring the dawn chorus in tropical areas, since birds deal with a reduced degree of seasonal variability (Dorado-Correa et al. 2016).

Airport noise is an extreme type of noise pollution with high amplitude across a wide spectrum of frequencies and is usually predictable in time, given its dependency upon scheduled flights (Sierro et al. 2017). Birds living near airports have been found to anticipate their dawn song, avoiding early morning aircraft peak traffic periods (Gil et al. 2015; Dominoni et al. 2016; Sierro et al. 2017). Thus, it appears that at least some species can adjust their singing periods to avoid the interference of anthropogenic noise. Species that are unable to adjust their behavior may be more susceptible to the impact of noise in their population dynamics, and indeed studies show that some species in noisy places face reduced pairing success (Habib et al. 2007), as well as reduced population density (Bayne et al. 2008). At chronic noise levels, species can either avoid or, if they remain in the noisy area, face the negative resulting consequences (Kleist et al. 2018; Injaian et al. 2019).

Here, we test whether bird populations living near tropical airports exhibit an advance in dawn song onset time in comparison with control populations at quieter sites, thus avoiding the possible interference caused by aircraft traffic. We predict that species with higher song frequencies and a lower degree of urbanity will not respond as strongly to airport noise, and that changes in dawn song onset time will be a positive function of the amount of noise avoided by singing at a different time.

Methods

Study sites

We collected acoustic data in three regions in Brazil (Brasília, Campinas, and Salvador). Each studied region comprised one
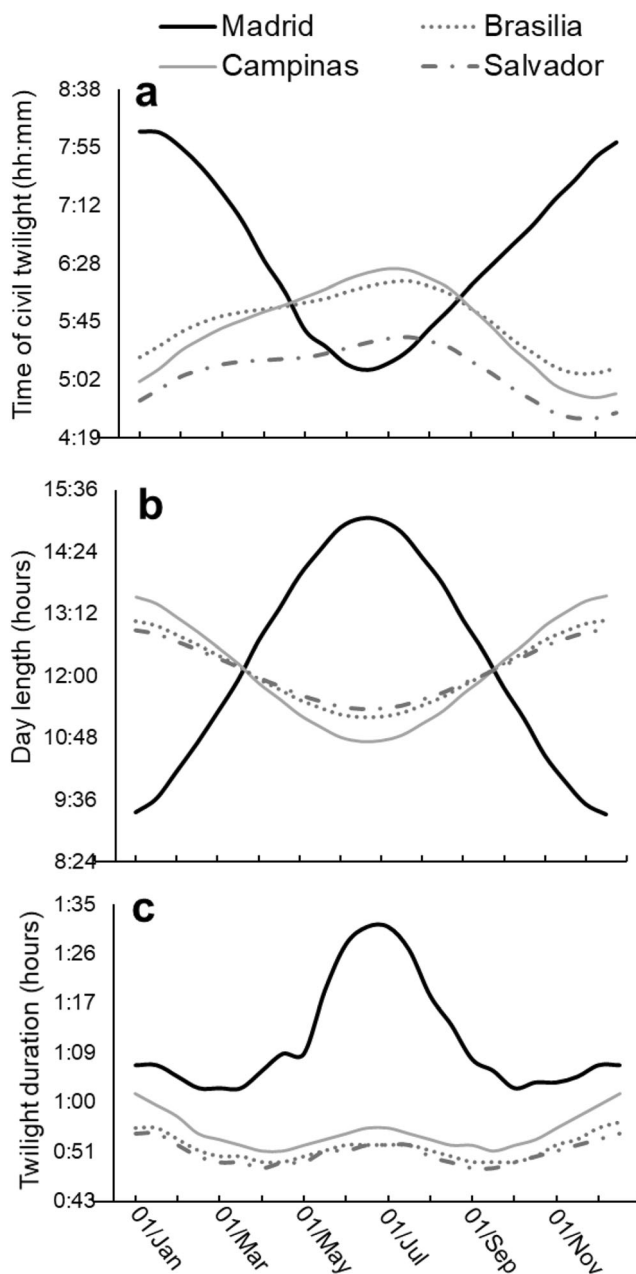
Fig. 1 Sunlight seasonal variation across a year for sites in three tropical regions (Brasília = 2014; Campinas = 2014; and Salvador = 2015; color = grey) and in one temperate region (Madrid = 2014; color = black). **a** Variation in time of civil twilight. **b** Variation in day length. **c** Variation in twilight duration (astronomical twilight time *minus* civil twilight time). Data obtained from https://www.timeanddate.com/sun/

airport-affected site and one quiet control site (Fig. 2). The airport-affected sites were located around the lanes of three major airports in Brazil, where we found disturbed native vegetation, high levels of noise, and influence of artificial light. More detailed description of areas can be found in Alquezar et al. (2020). The "Presidente Juscelino Kubitschek International Airport" (AIR_Bras: 15° 52′ 19.4″ S 47° 55′ 11.9″ W) and its quiet control site (CONT_Bras: "Brasilia National Park" - 15° 43′ 18.1″ S 47° 58′ 14.4″ W)

were located in Brasília's region (Fig. 2a). The "Viracopos International Airport" (AIR_Camp: 23° 00′ 24.4″ S 47° 08′ 30.0″ W) and its quiet control site (CONT_Camp: private farm - 23° 05′ 53.2″ S 47° 07′ 49.8″ W) were located in Campinas' region (Fig. 2b). And finally, the "Luís Eduardo Magalhães International Airport" (AIR_Sal: 12° 54′ 42.8″ S 38° 19′ 44.2″ W) and its respective quiet control site (CONT_Sal: residential area with protected natural areas - 12° 51′ 30.0″ S 38° 16′ 08.0″ W) were located in Salvador's region (Fig. 2c).

Airport activity began at different times for each region. In Brasília (AIR_Bras), activity started between − 60 and 0 min relative to civil twilight, during which there were at least 9 flights/h (see definition in ESM 1); in Campinas (AIR_Camp), activity started between − 120 and − 60, during which there were at least 8 flights/h; and in Salvador (AIR_Sal), activity was more intense during the night than in the other airports, and presented a decreased activity between − 120 (8.8 flights/h) and 0 (2.5 flights/h) minutes relative to civil twilight. Airport activity details are provided in ESM 1 (Table S1, Fig. S1).

Recordings

We used Automatic Recording Units (ARUs; SONGMETER SM2+; Wildlife Acoustics 2007) to record the birds' dawn singing. These devices were programmed to record from 2 h before civil twilight (− 120 min) until 1 h after civil twilight (60 min), alternating periods of 1 min of recording and 1 min of inactivity. Recorders were set in custom-made harnesses and hung from branches at a height of 1–3 m (Gil et al. 2015). As twilight timing differed among studied regions due to differences in longitudinal location, we standardized time, such that "0" was the time when the sun's center was 6 degrees below the horizon (Miller 2006; Nordt and Klenke 2013; Time and Date AS 2019). ARUs worked in stereo mode, at a sample rate of 44.1 kHz and 16 bits.

Studied sites were sampled during the breeding season for each region (Repenning and Fontana 2011; Marini et al. 2012; França et al. 2016), when birds have their highest vocal activity. Recorders were installed simultaneously in the paired sites (airport and control) within each region, to avoid possible seasonality effects (see Nordt and Klenke 2013). In Brasília, we placed recorders in 12 points in the airport-affected site, and 12 points in the quiet control site, between October 10 and 27 of 2014. In Campinas, we placed recorders in 12 points in the paired sites between December 5 and 19 of 2014. And finally, in Salvador, we had a smaller area available in the airport-affected site, so we placed recorders in 10 points in both airport-affected and quiet sites between December 19–23 of 2015 and January 6–16 of 2016. For all regions, each recording point was located at least 250 m from other points and was sampled during two consecutive mornings. Points in
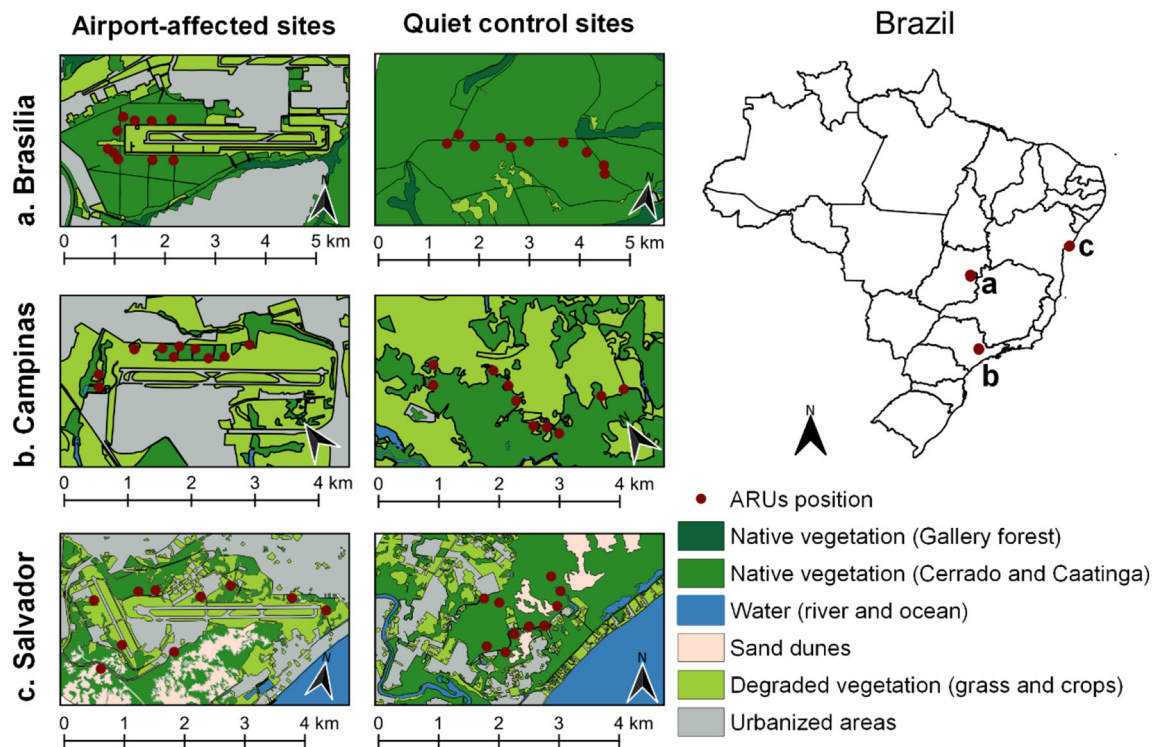
Fig. 2 Location of study sites in Brazil, including airport-affected (AIR) and quiet control (CONT) sites for each studied region (Brasília, Campinas, and Salvador). For each studied site, we present a landscape sketch and the Automatic Recorder Unit's position

airport-affected sites were at a maximum distance of 300 m from airport lanes. See Fig. 2 and ESM 2 (Table S2) for geographic coordinates of recorders.

We used Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY) for screening and listening to the recordings. For each morning, we identified the time of first and second song of each species. For statistical analysis, we did not consider species that were recorded in fewer than eight sampled points, due to excessively low sample size. Observer bias in the field was minimized by using automatic recording units, avoiding the disturbance to birds' behavior and reducing observer error (Alquezar and Machado 2015). The process of screening and listening to the recordings was not blinded with respect to the site, since the observer (RDA) could identify whether recordings were from airport or quiet sites.

Statistical analyses

Species responses We fitted a linear mixed model (LMM–global model 1), using "Dawn song onset time" as response variable (untransformed data) and "Point" (geographical location of each recorder) as random effect. The interaction between variables "Site-type" (airport-affected or quiet control) and "Species" was included as predictor, and variable "Region" was included as a covariate. The significance value (p) was calculated with a post hoc analysis of deviance (type III). Subsequently, we fitted a LMM for each species to assess species-specific responses, using

the same previously described model structure. To run these analyses, we used packages "*AID*" (Asar et al. 2017), "*lmerTest*" (Kuznetsova et al. 2017), "*lme4*" (Bates et al. 2015), and "*car*" (Fox and Weisberg 2011). Statistical analyses were performed in R version 3.3.2 (R Core Team 2019) and significance was considered for $p < 0.05$.

Population responses We defined one population-specific variable (difference in dawn song onset time; ESM 3: Table S3), three species-specific variables (song frequency, degree of urbanity, and eye size; ESM 3; Table S3), and two environmental variables (noise release and light pollution; ESM 3; Tables S4, S5), to be used in a meta-analytic approach to understand population responses (Table 1). We evaluated population responses ($N = 25$) considering that noise and light differed among regions.

We transformed variables as standardized effect differences (SED - mean family), reflecting the variation between means and accounting for sample size (Hedges 2008). The formulas used are described in Nakagawa and Cuthill (2007):

$$\text{Hedge's } d = \frac{m_2 - m_1}{S_{\text{pooled}}}$$

$$S_{\text{pooled}} = \sqrt{\frac{(n_2-1)s_2^2 + (n_1-1)s_1^2}{n_1 + n_2 - 1}}$$

Table 1 Variables definition (global model 2)

Variable/formula	Description	Interpretation
A. Population-specific		
Difference in dawn song onset time(dependent variable)		
SED (time at airport - time at control)	Reflects the difference of population's timing for first song in airport-affected and quiet control sites (advances and delays)	> 0 = advance < 0 = delay
B. Species-specific		
Song frequency (predictor)		
Mean values for each species	The frequency in which species concentrate most of the song energy (peak frequency)	
Degree of urbanity (predictor)		
Species occurrence (presence/absence) in Brazil using the eBird database	Degree of association of each species to urban environments	> 0 = more urban < 0 = less urban
Eye size (covariate)		
Mean values for each species	Species eye size (related to time of dawn song onset). Corrected by body weight	
C. Environmental		
Noise release (predictor)		
SED (noise airport (dawn singing time: airport) - noise airport (dawn singing time: control))	Amount of noise avoided by singing in a different time (freq range = 2–10 kHz)	> 0 = effective (reduced noise) < 0 = not effective (increased noise)
Light pollution (covariate)		
SED (darkness control (time: control) - darkness airport (time: control))	The difference in light intensity between airport-affected and quiet control sites at night-time	> 0 = more luminous < 0 = less luminous

SED, standardized effect difference

where m_1 and m_2 are means of compared groups and S_{pooled} is the pooled standard deviation, n_1 and n_2 are sample sizes, and s^2 is variance. Details relative to methodologies for collection of variables, determination of raw means, and calculation of standardized effect sizes are available in ESM 3.

Using these variables, we fitted a new LMM (global model 2), to understand whether "difference in dawn song onset time" could be explained by species-specific (song frequency and degree of urbanity) and environmental characteristics (noise release), using "Species" as random effect. Variables "Eye size," "Light pollution," and "Region" were included as covariates. Given the exploratory character of this analysis, we used "dredge" and "model average" functions to summarize the best models, ranking them by increasing Akaike's Information Criteria (AICc) and considering models within ΔAIC < 2. All continuous data were normalized using boxcox transformation, after re-scaling to avoid negative values. To run these analyses, we used the additional packages "*MuMIn*" (Barton 2016) and "*AICcmodavg*" (Mazerolle 2016).

We predicted that differences in the direction and strength of change (advances or delays) could be explained by the following: (a) song frequency: we expected birds with lower song frequencies to show greater advances than birds with higher song frequencies (Rheindt 2003; Francis et al. 2011), due to occurrence of greater noise masking in lower frequencies; (b) species-specific degree of urbanity: we expected urban adapter species to show greater advances than urban avoiders (Croci et al. 2008), since we assume that these species are better prepared to cope with urban noise pollution; and (c) noise release: we expected differences in singing time to be positively related to the amount of noise avoided.

Results

We obtained dawn song onset data in airport-affected and quiet control sites for 15 species (order Passeriformes), including oscines and suboscines (Table 2). The most representative family was Tyrannidae, with 7 species. Some species were recorded in all three studied regions (Brasília, Campinas, and Salvador), while others occurred in either one or two regions. Here, we considered species that sing early in the morning, including those that sing before twilight (typically described as dawn song) as well as those that initiate singing after civil twilight (Dominoni et al. 2016).

In the three studied regions, noise levels were higher in the airport-affected than in the quiet control sites and increased progressively with time (Fig. 3). However, there were differences between areas. In the Campinas region, we observed the greatest difference in noise levels between the quiet control

Table 2 Mean values of dawn song onset time for 15 species (in minutes relative to twilight), for airport-affected and quiet control sites, including sample size (N = number of points). Region refers to populations included in sample (B = Brasília, C = Campinas, S = Salvador, and ALL = all regions)

Family	Species	Region	Airport		Control	
			Mean	N	Mean	N
Suboscines						
Dendrocolaptidae	*Lepidocolaptes angustirostris*	B	6.37	12	− 1.87	13
Furnariidae	*Furnarius rufus*	C, S	15.03	17	25.58	17
Tyrannidae	*Camptostoma obsoletum*	ALL	29.07	10	16.75	20
	Elaenia flavogaster	ALL	9.91	14	16.00	14
	Elaenia cristata	B, S	23.07	12	30.97	19
	Elaenia chiriquensis	B, C	− 15.30	14	− 0.69	12
	Myiarchus swainsoni	B, C	1.88	10	7.22	15
	Pitangus sulphuratus	C, S	36.95	20	36.19	15
	Tyrannus melancholicus	C, S	4.97	20	10.33	14
Oscines						
Vireonidae	*Cyclarhis gujanensis*	C, S	20.56	14	18.19	22
Troglodytidae	*Troglodytes musculus*	B, C	24.30	11	8.23	23
Turdidae	*Turdus leucomelas*	ALL	4.00	20	− 1.03	24
Passerellidae	*Zonotrichia capensis*	C	10.48	11	− 3.08	12
Thraupidae	*Neothraupis fasciata*	B	− 10.10	12	− 2.86	10
	Tangara sayaca	C, S	12.18	21	13.41	17

and the airport-affected sites (approx. 13 dB). The observed difference in Brasília was close to Campinas' value (approx. 12 dB), and the lowest difference was observed in Salvador (approx. 8 dB).

The results of the global model testing the full dataset (global model 1), showed a significant interaction effect between "Site-type" and "Species" (post hoc Anova: X^2 = 60.09, df = 14, p < 0.001), indicating a heterogeneity of responses instead of the general predicted advance. In other words, the difference in timing between airport and control was different depending on the species. As previously known, the covariate "Region" was also significant in the model (post hoc Anova: X^2 = 17.62, df = 2, p < 0.001) (model details available in ESM 4; Tables S6, S7, Fig. S3).

Species-specific LMMs identified two species anticipating dawn song onset in noisy sites (Table 3, Fig. 4): the white-banded tanager (*Neothraupis fasciata*; on average 8.8 min earlier in airport; p < 0.001) and the lesser elaenia (*Elaenia chiriquensis*; on average 14.6 min earlier; p = 0.001). In the opposite direction, four species presented a significant delay, with later song onset time in noisy sites: the southern beardless-tyrannulet (*Camptostoma obsoletum*; on average 12.3 min later; p = 0.005), the southern house wren (*Troglodytes musculus*; on average 16 min later; p = 0.01), the rufous-collared sparrow (*Zonotrichia capensis*; on average 13.5 min later; p < 0.001), and the pale-breasted thrush (*Turdus leucomelas*; on average 5 min later; p = 0.03). The remaining nine species presented no significant changes (model details available in ESM 5; Table S8).

According to the global model 2, based on population data (N = 25) and following a meta-analytic approach, changes in dawn song onset time were not explained by any of our predictors (song frequency, degree of urbanity, and noise release; Table 4). The models with ΔAIC > 2 included some of our covariates (light pollution and region). When the combination of the two best models was summarized in the average model, none of the variables presented significant differences. The other selected models presenting ΔAIC > 2 were not considered as suitable explanations for dawn song onset time changes (model details available in ESM 6; Tables S9, S10, Fig. S4).

Discussion

Our results showed that species-specific dawn song onset times were not globally affected by exposure to airport noise in a sample of Neotropical bird species. We found that responses to airport noise were species-specific, region-specific, and highly variable. In our global analysis, none of our tested predictors explained the direction of the changes.

Contrary to our first hypothesis, the majority of evaluated species did not show a change in dawn song onset in the expected direction (song advance). The significant interaction between "Site-type" and "Species" shows that species responded in a heterogeneous fashion (advances and delays). Previous studies in Europe have found that timing modifications involved advances in singing time (Gil et al. 2015;
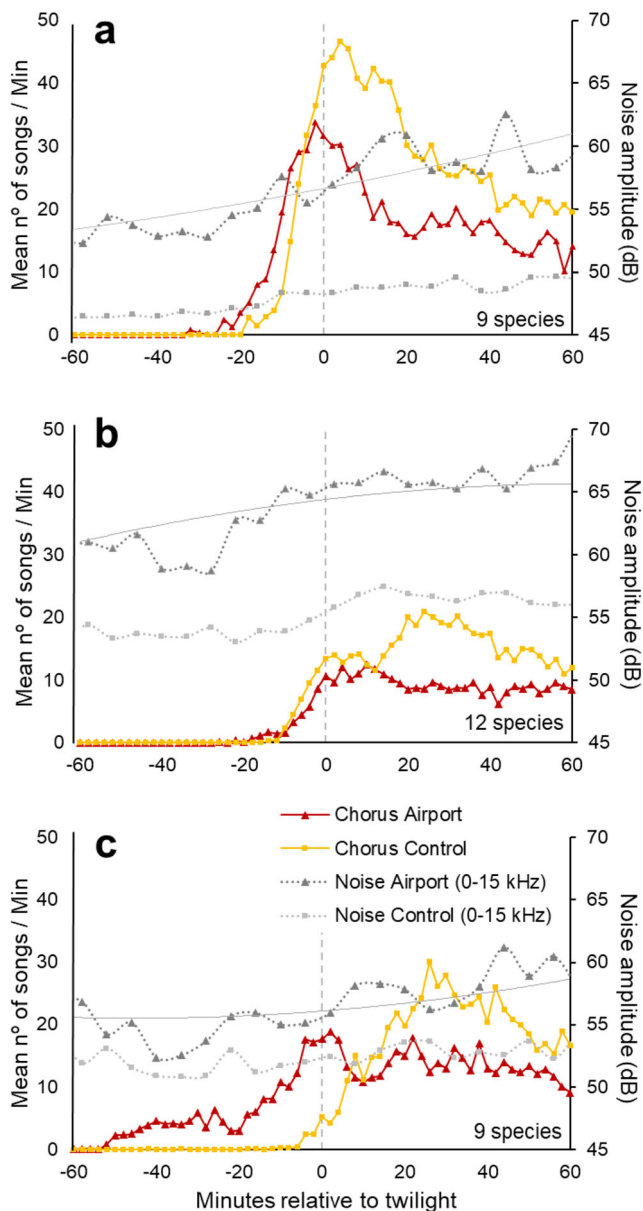
Fig. 3 Regional dawn chorus scenario. Left y-axis shows mean number of songs per minute, considering the analyzed species in each region. Red lines refer to dawn chorus at airport-affected and orange lines to quiet control sites. Values were estimated by the sum of number of songs produced by all species in each morning. The presented values are means per morning. Right y-axis shows mean noise amplitude (dB; re. 20μPa) at airport-affected (dark grey, upper lines) and quiet control sites (light grey), considering the whole range of frequencies (0–15 kHz). (a) Brasília, (b) Campinas, and (c) Salvador regions

Dominoni et al. 2016), although some species presented no significant changes in their dawn song timing. In our study in Brazil, however, heterogeneity was the norm, with variable responses indicating that species respond differently to the same habitat disturbance.

When we analyzed species separately, we found that 6 of the 15 analyzed species presented changes in their dawn song

onset time. Both oscines and suboscines presented advances and delays in dawn chorus timing. Although advances are documented in airport environments (Gil et al. 2015; Dominoni et al. 2016; Sierro et al. 2017), no previous study has found species delaying their dawn chorus onset time. Studies have shown that suboscines may have less plasticity in their songs (Ríos-Chelén et al. 2012) due to a lower ability to learn new songs and to change repertoire during their lifetime, but this idea has been revisited and questioned (Tobias et al. 2012; Freeman et al. 2017). Here, the oscine (*N. fasciata*) and the suboscine (*E. chiriquensis*) that advanced their dawn chorus have a specific song during dawn and dusk chorus, and this song is not sung during other times of the day. This could be an important factor determining the advance, since they are time-constrained to communicate this specific social information.

To further investigate the observed shifts in dawn song onset times, we tested whether song peak frequency, species degree of urbanity, and noise release may predict the direction of the dawn song onset time changes. However, none of these predictors explained the observed changes. We expected that birds with lower song frequencies would show greater advances in dawn song than birds with higher song frequencies (Rheindt 2003; Francis et al. 2011; Stanley et al. 2016). However, no influence of song frequency was found. Unlike traffic noise (Slabbekoorn 2013), airport noise affects such a wide frequency spectrum (Sierro et al. 2017) that differences in avian song frequency may be useless to avoid noise masking. We estimated the degree of urbanity for each species, and used that estimate to test whether more urban species would show greater advances in dawn song than less urban species (Croci et al. 2008). However, this predictor was also not relevant, suggesting that the capacity to invade urban habitats is not explained by plasticity in song timing.

We also expected that the amount of noise avoided by changing singing time would be a factor that could explain how much earlier a species sang. However, the dawn song onset time was not explained by the amount of noise that birds could avoid by singing at a different time. This is in contrast to a recent study in which seasonal differences in song advance were explained by differences in the overlap of natural song routines with airport traffic noise (Sierro et al. 2017). It is possible that this result could be explained by differences in airport noise patterns with respect to previous studies. In this study, noise levels at airport-affected sites were higher than in quiet control sites even during dawn time, indicating a substantial level of airport noise activity at this time. This is also in contrast to previous studies, in which very low mean noise amplitudes (46 ± 12 dB) at dawn time were reported in the airport (Dominoni et al. 2016). This early airport activity in our study sites might be a barrier for birds to change their dawn song timing, as birds living in airport-environments with air traffic starting markedly before dawn may not be able to
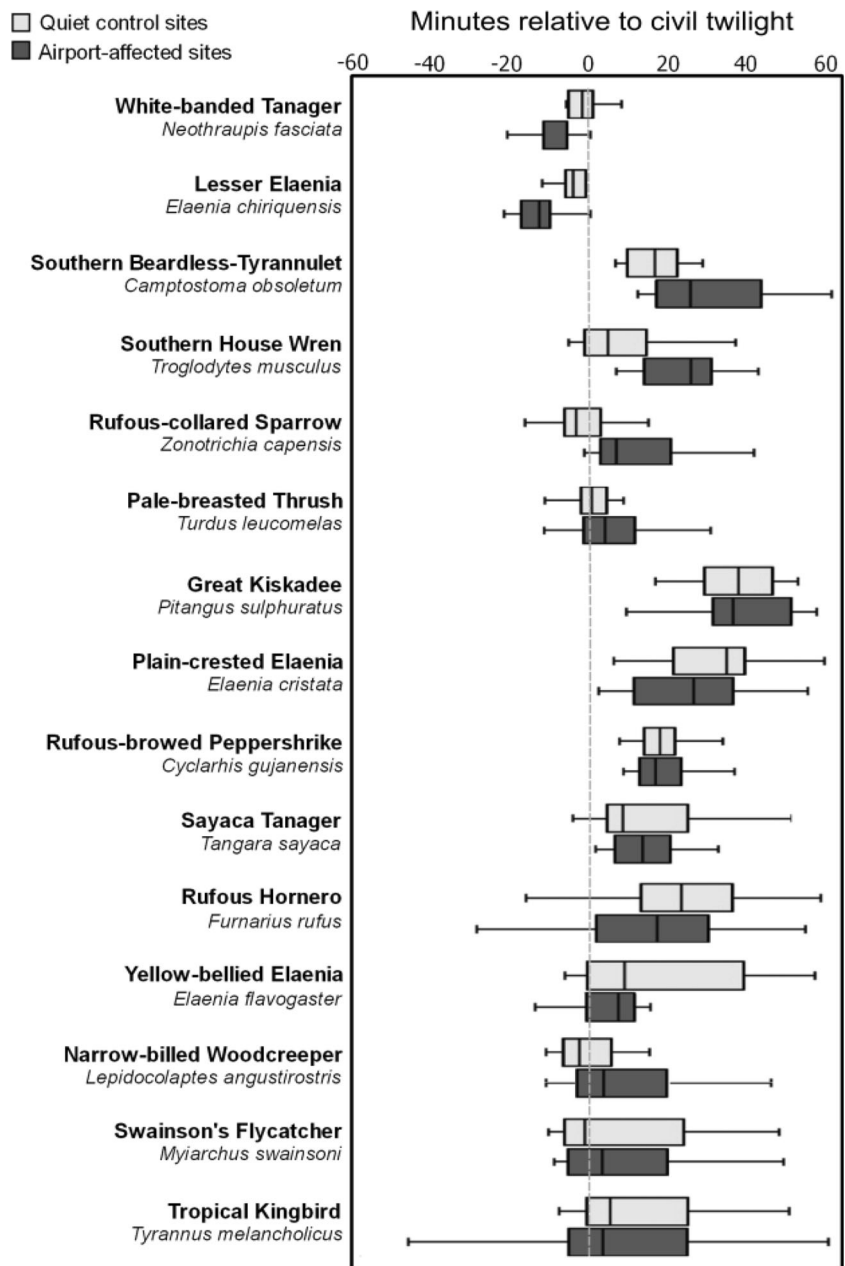
Table 3 Dawn song onset time per species, analyzed by LMM (recorder point as random effect). The *p* value was determined through post-hoc analysis of variance. Species are presented in phylogenetic order

	Estimate	SE	X^2	df	p
1. Lepidocolaptes angustirostris					
Intercept	− 1.22	3.26	0.14	1	0.70
Site_type Airport	8.15	4.60	3.13	1	0.07
2. Furnarius rufus					
Intercept	28.44	5.16	30.33	1	< 0.001
Site_type Airport	− 10.32	5.88	3.07	1	0.07
Region	− 5.34	5.88	0.82	1	0.36
3. Camptostoma obsoletum					
Intercept	13.47	3.31	16.58	1	< 0.001
Site_type Airport	11.85	4.26	7.71	1	0.005
Region	Not applicable		13.08	2	0.001
4. Elaenia flavogaster					
Intercept	60.77	21.94	7.66	1	0.01
Site_type Airport	− 0.67	7.90	0.73	1	0.39
Region	Not applicable		4.65	2	0.09
5. Elaenia cristata					
Intercept	28.88	3.58	65.09	1	0.001
Site_type Airport	− 4.06	5.10	0.63	1	0.42
Region	9.84	6.10	2.60	1	0.10
6. Elaenia chiriquensis					
Intercept	− 0.20	3.63	0	1	0.95
Site_type Airport	− 16.7	5.09	10.75	1	0.001
Region	12.27	9.39	1.70	1	0.19
7. Myiarchus swainsoni					
Intercept	− 1.54	8.08	0.03	1	0.84
Site_type Airport	0.72	11.26	0	1	0.94
Region	29.68	12.36	5.761	1	0.01
8. Pitangus sulphuratus					
Intercept	42.02	3.42	150.76	1	< 0.001
Site_type Airport	− 0.05	3.43	0	1	0.98
Region	− 9.04	3.42	6.96	1	0.008
9. Tyrannus melancholicus					
Intercept	12.05	7.86	2.35	1	0.12
Site_type Airport	− 3.76	7.86	0.22	1	0.63
Region	2.43	7.76	0.09	1	0.75
10. Cyclarhis gujanensis					
Intercept	23.40	2.03	131.71	1	< 0.001
Site_type Airport	5.41	2.78	3.77	1	0.052
Region	− 10.94	2.74	15.90	1	< 0.001
11. Troglodytes musculus					
Intercept	3.40	3.39	1.00	1	0.32
Site_type Airport	11.75	4.87	5.82	1	0.01
Region	12.15	4.55	7.12	1	0.007
12. Turdus leucomelas					
Intercept	3.84	4.37	0.77	1	0.37
Site_type Airport	5.64	2.65	4.51	1	0.03
Region	Not applicable		11.45	2	0.003
13. Zonotrichia capensis					
Intercept	− 2.78	2.61	1.13	1	0.28
Site_type Airport	13.33	3.83	12.08	1	< 0.001
14. Neothraupis fasciata					
Intercept	− 2.91	1.37	4.47	1	0.03
Site_type Airport	− 7.09	1.80	15.42	1	< 0.001
15. Tangara sayaca					
Intercept	14.34	3.94	13.23	1	< 0.001
Site_type Airport	− 0.93	4.67	0.04	1	0.84
Region	− 0.90	4.71	0.03	1	0.84

escape from airplane noise. Noticeably, the only two species anticipating dawn song in our study are in the Brasília region, where air traffic activity starts later than in the other studied airports.

The differences between our current findings and those of previous studies (Gil et al. 2015; Dominoni et al. 2016; Sierro et al. 2017) can also reflect a geographical context. All previous studies of airport noise effects were conducted in

Fig. 4 Dawn song onset time for 15 bird species, in airport-affected sites (darker) and quiet control sites (lighter). The first six species presented significant shifts in dawn song onset time. The boxes show the median, interquartile range, and whiskers (indicating the 90th and 10th percentiles)

temperate regions, whereas in our case, we addressed this issue in tropical landscapes. It is possible that reduced

seasonal variations of light in tropical areas and lower dependence of birds upon photoperiodic cues for breeding cycles (Moore et al. 2005) may reduce the scope of behavioral plasticity in birds' dawn song in tropical regions (Dorado-Correa et al. 2016; Marín-Gómez and MacGregor-Fors 2019).

An important issue that should be addressed in future studies is whether changes in dawn song onset time can be related to density or population size. Several studies have shown that reduced avian breeding success can be related to exposure to noise (Habib et al. 2007; Francis et al. 2009; Halfwerk et al. 2011), leading to changes in population and community dynamics (Bayne et al. 2008; Proppe et al. 2013; Slabbekoorn 2013) and biotic homogenization at airports (Alquezar et al. 2020). Also, the dawn chorus is assumed to function as a

Table 4 Selected models (LMM) for effects of "song frequency," "degree of urbanity," and "noise release" in "difference in dawn song onset time." Variables "eye size," "light pollution," and "region" were included as covariates, "species" was included as random effect. Intercepts and confidence intervals for averaged models with ΔAIC < 2 provided in Electronic Supplementary Material 5

Selected models	df	AICc	ΔAIC	Weight
Light pollution	4	72.8	0.00	0.250
Region	5	73.3	0.48	0.196

mechanism for territory defense and maintenance of social dynamics (Kacelnik and Krebs 1982; McDonald 1989; Staicer et al. 1996; Shimmura et al. 2015). Thus, it is possible that delays in dawn song onset time could be explained by reductions in population size of airport species, since lower competition could lead to lower effort to sing as early as possible to acquire mates or defend territories (Foote et al. 2011).

Our evidence suggests that tropical bird species differ from temperate species in their behavioral responses to the disturbances of airports. In summary, we rejected the hypothesis that extreme noise affects dawn song onset of all species in a uniform manner. Instead, we show that noise affects species in specific ways, leading either to advances or delays in their usual timing. Possibly, differences in airport activity and shorter variations in day length and in twilight time/duration in tropical areas may reduce the window of opportunity for birds to change their dawn song timing. We encourage subsequent studies to explore the possible relationship between population declines (due to reproductive challenges) and reduced competition with dawn singing behavior in noisy environments.

Compliance with ethical standards All authors agreed with the content of this manuscript and made substantial contributions to the conception, design of the work, analysis, and/or interpretation of data.

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