Urban cycles of human activity do not significantly alter the behaviour of a duetting bird

PEDRO DINIZ,*[1,2] (iD) EDVALDO F. SILVA-JR[1,2] (iD) & REGINA H. MACEDO[2] (iD)

[1]*Programa de Pós-Graduação em Ecologia, Universidade de Brasília, Brasília, DF, 70910-900, Brazil*

[2]*Laboratório de Comportamento Animal, Departamento de Zoologia, Universidade de Brasília, Brasília, DF, 70910-900, Brazil*

The weekend effect hypothesis predicts that weekly cycles of human activity impact animal behaviour and physiology. This hypothesis has been supported in the context of recreational activity in natural environments but it is unknown whether it also applies to urban animals. We tested this hypothesis by comparing the sentinel (territorial vigilance), foraging and vocal behaviours of an urban-dwelling bird, the Rufous Hornero *Furnarius rufus*, between weekdays and weekends (and holidays) within a university campus in central Brazil. The level of human activity (noise, traffic and pedestrian flow) increases greatly on weekdays on this campus. We predicted that the birds would perceive a greater predation risk and would need to adjust their acoustic signals in response to anthropogenic noise on weekdays. Thus, we expected that the birds would spend more time as sentinels and less time foraging, and would sing for longer periods and at a higher pitch on weekdays than on weekends. We also expected weaker duet responsiveness (answering partner-initiated song) on noisier weekdays than on weekends, assuming that noise would disrupt signal transmission between partners. We found that birds spent slightly more time (~ 4%) in sentinel behaviour and less time (~ 2–5%) foraging on weekdays than on weekends, but these effects were small and not statistically significant. Birds were equally likely to sing solos, start duets and answer partner-initiated duets on weekends and weekdays. Finally, phrase duration and acoustic parameters of duets were similar on weekends and weekdays. Our results provide little support for the weekend effect hypothesis, suggesting that these urban-dwelling birds may be habituated or indifferent to periodic variation in human activity levels.

Keywords: bird song, *Furnarius rufus*, human disturbance, noise, Rufous Hornero, urban ecology, weekend effect hypothesis.

Human activity, including recreational events (Blumstein *et al.* 2017) and flow of people (Wu *et al.* 2014), are temporally dynamic and may have weekly cycles (Cerveny & Balling 1998, Nix *et al.* 2018). Human activity levels tend to increase during weekends in natural environments and urban parks (Pelletier 2006, Casas *et al.* 2016), whereas they may decrease in urban areas (Fokidis *et al.* 2011). The weekend effect hypothesis (Stalmaster & Kaiser 1998) predicts that these weekly cycles

of human activity affect the physiology and behaviour of non-human animals (Bautista *et al.* 2004, Tarjuelo *et al.* 2015, Casas *et al.* 2016).

Wild animals respond to more intense periods of human activity levels by exhibiting higher levels of vigilance (Tarjuelo *et al.* 2015), flushing (Lafferty 2001) or fear-related behaviour (Nix *et al.* 2018). Because foraging often has a trade-off with vigilance, behavioural changes due to human activities may result in less time spent foraging (Payne *et al.* 2014), use of low-quality areas and higher energy expenditure on days with more human disturbance (Tarjuelo *et al.* 2015). For example, Bonelli's Eagles *Aquila fasciata* increase their

*Corresponding author.
Email: pdadiniz@gmail.com
Twitter ID: @pdadiniz

home-range sizes during weekends and holidays, when human activity is highest (Perona *et al.* 2019), and Little Bustards *Tetrax tetrax* increase their foraging effort after weekends, probably as a strategy to compensate for the increased energy expenditure on days with higher levels of human activity (Tarjuelo *et al.* 2015).

Human activity can also promote changes in avian vocal behaviour (Brumm 2004, Diaz *et al.* 2011, Silva *et al.* 2014). Song is crucial for territory defence and mate attraction in birds (Catchpole & Slater 2008). However, in response to human activity, birds may reduce their singing effort (Gutzwiller & Anderson 1994) due to human-induced increase in vigilance (Frid & Dill 2002, Campos *et al.* 2009). In addition, anthropogenic noise can hamper the transmission of bird song (Nemeth & Brumm 2010). Consequently, birds may avoid singing during rush hours or, conversely, sing more frequently (Brumm & Slater 2006) at a higher amplitude, frequency, tonality (Hanna *et al.* 2011) and for greater durations to improve song redundancy and transmission in noisy conditions (Shannon *et al.* 2016, Potvin 2017). For example, roadside Common Reed Buntings *Emberiza schoeniclus* reduce song rate and increase minimum frequency of their songs on noisy days compared with quiet days (Gross *et al.* 2010).

Most studies involving the behavioural response of animals to human activities have focused on the effects of tourism on wild animals in natural habitats (Blumstein *et al.* 2017) or on the effects of anthropogenic noise on wild animals (Shannon *et al.* 2016). In addition, most studies of noise effects on bird song have been conducted by comparing rural and urban populations or based on existing acoustic gradients over space (Shannon *et al.* 2016). In contrast, little is known about whether weekly cycles of human activities affect the behavioural time-budget (Fernández-Juricic & Tellería 2000, Stofberg *et al.* 2019) and song structure (Gross *et al.* 2010) of urban species.

In this study, we hypothesized that urban birds will respond to weekly cycles of human activity by changing their behaviour and singing patterns. To compare human-induced changes in animal behaviour between weekdays and weekends, we can test for factors that often vary in a weekly cyclical fashion, such as human presence (Fernández-Juricic & Tellería 2000), traffic flow (Williams *et al.* 1998, Gross *et al.* 2010) and anthropogenic noise

(Brumm 2004, Halfwerk *et al.* 2011b, Gentry *et al.* 2017), while controlling for within-individual variation and other factors that vary spatially and do not have weekly patterns, such as habitat structure (Diaz *et al.* 2011) and light pollution (Silva *et al.* 2014).

To test our hypothesis, we used a Neotropical bird, the Rufous Hornero *Furnarius rufus*, as a model species. This species is abundant in urban areas across southern South America (Sick 2001, Fontana *et al.* 2011, Remsen & Bonan 2020). We evaluated whether individuals change their behaviours (sentinel, foraging, territorial and vocal behaviours) in response to weekly variation in human activity levels. The Rufous Hornero is a ground-foraging species in which socially monogamous pairs sing simultaneous medium-frequency broadband duets (~ 2–6 kHz; overlapped sex-specific phrases) to defend year-round territories and the pair-bond (Roper 2005, Diniz *et al.* 2018, 2019, 2020, Mentesana *et al.* 2020). We studied territorial pairs in a population inhabiting a university campus in central Brazil (Diniz *et al.* 2016, 2018). Human activity at the university is typically higher on weekdays (from Monday to Friday) than on weekends and holidays (Aruwajoye 2016).

We compared sentinel, foraging and vocal behaviour between weekdays (high human activity) and weekends and holidays (low human activity) during the academic semester. If human presence impacts bird behaviour, we expected that birds would increase sentinel effort and decrease foraging on weekdays in comparison with the weekends and holidays. This prediction assumes that human presence would increase perceived predation risk (Beale & Monaghan 2004), resulting in higher sentinel effort (Tarjuelo *et al.* 2015) and reduced foraging (Payne *et al.* 2014). If human-induced noise impacts bird vocal behaviour, we expected higher-pitched, tonal (i.e. narrow frequency bandwidth) and longer songs, and higher singing effort on weekdays than on weekends and holidays. These vocal adjustment strategies are expected because they improve acoustic signal propagation in noisy conditions by avoiding masking and increasing signal redundancy (Hanna *et al.* 2011, Shannon *et al.* 2016, Potvin 2017). Additionally, we assumed that anthropogenic noise on weekdays would mask bird song and prevent partners from hearing or identifying each other. Thus, we expected weaker duet responsiveness (answering partner-initiated songs) on weekdays than on weekends.

METHODS

Study area and procedures

We conducted this study in a 175-ha section of the campus Darcy Ribeiro of the Universidade de Brasília, Brazil (15°45'S, 47°52'W). The campus has an area of ~ 400 ha and a human population size of ~ 50 000 people (data compiled from 2016) (Werneck & Arruda 2017). According to a survey, there are four times as many people transiting within the campus on weekdays than on weekends, and 45% of them use private motor vehicles (Aruwajoye 2016).

We monitored sentinel and foraging behaviours of 11 Rufous Hornero social units over 7 months (June–December) and one additional social unit was monitored for 3.5 months (June–September) in 2015. In this species, young may stay in their parents' territories for one non-breeding season (Diniz *et al.* 2018). Social units were composed of a breeding pair with or without juveniles. The study period encompassed both the breeding and the non-breeding seasons and all studied adults were banded (details in Diniz *et al.* 2018). Song and territory data were already available in the dataset generated by previous studies (Diniz *et al.* 2018, 2020).

Human activities

We regarded 'human activity level' as a factor consisting of two levels: low human activity on weekends (Saturday and Sunday) and holidays (weekends hereafter), and high human activity on weekdays (Monday to Friday). The long academic holidays occurred from 12 July to 8 August (dry season) and from 15 December to 30 December (wet season) in 2015 ($n = 33$ observations, 12 social units, 17 days). Public holidays occurred on 4 June and 7 September ($n = 4$ observations, 4 groups, 2 days).

To validate our classification (weekends vs. weekdays), we estimated human activity levels within the studied territories and in the main parking lots of the campus. First, we estimated levels of three human activity types at the studied territories for each subject pair: (1) number of pedestrians plus cyclists, (2) number of vehicles and (3) ambient noise. This sampling was carried out over 5 min, twice at each territory, in 2017: once on a weekday (Wednesday 30 August) and once on a

weekend day (Sunday 27 August or Saturday 2 September) (adapted from Fernández-Juricic and Tellería, 1999, Wang *et al.* 2015). Although the samples were not collected at the same time of day on weekdays (07:41–10:16 h) and weekends (10:30–16:42 h), we included the time of day in the statistical models. Although we sampled bird behaviour in 2015 and human activity in 2017, human population size on campus increased by only 3% between 2015 and 2017 (Supporting Information Fig. S1), and the physical environment of the territories did not vary between the two years, as shown by satellite images (Supporting Information Appendix S1).

We counted the number of pedestrians and cyclists who passed through the perimeter of each territory, and the number of vehicles that drove along the main road closest to each territory. Roads were located along territory borders ($n = 8$ territories) or through territories ($n = 2$ territories). We assigned zero vehicles for two territories that were distant from any roads (136 and 193 m away from the closest road). We measured sound pressure levels (SPL) with an SPL meter (SEW 2310SL, SPL range: 30–80 dBA) in the vicinity of the nest substrate structure (tree or light pole) at 20-s intervals for 0–5 min ($n = 16$ measurements). We used these SPL measurements to calculate the A-weighted equivalent continuous sound level in decibels (LAeq).

We also estimated the number of vehicles parked in each of three of the main campus parking lots (Aruwajoye 2016) (range: 1.80–3.71 ha) during weekdays ($n = 28$ days/ parking lot) and weekends ($n = 31$). We used satellite images from 2015 (from January to December) obtained from Google Earth (Supporting Information Fig. S2) to estimate the number of vehicles parked per day for each parking lot. We counted the number of parking rows that had more than 50% of their spaces occupied by vehicles, which we considered to be fully occupied. We then multiplied this value by the length of each parking row (in m) and the density of parking spaces per parking row (spaces/m).

Sentinel and foraging behaviours

Social units were observed for 1 h at ~ 15-day intervals, totalling 14 focal sessions for 11 groups, and seven focal sessions for one group that lost its territory (Diniz *et al.* 2018). We used

instantaneous sampling (Altmann 1974) to record four behaviour classes of each member of the pair: sentinel, foraging, nest building and parental care. The behaviours of juveniles were not quantified. Two observers separately recorded the behaviour of a different member of the pair at 1-min intervals during each focal session, allowing us to record the behaviours of the two birds simultaneously. We were able to monitor behaviours of focal females and males for an average ($\pm$ sd) of 54.78 $\pm$ 7.49 min per focal session and 54.57 $\pm$ 6.19 min per focal session ($n = 161$ focal sessions, 12 social units), respectively. Occasionally, we lost visual contact with the focal bird, for instance when it flew to neighbouring territories during chases or into dense tree canopies, or when the bird was behind buildings or cars. Songs and territorial disputes are often short in duration and infrequent (Diniz *et al.* 2018); thus, they were not included in the time budget.

The activity profile of the Rufous Hornero consists of alternating perching on trees or human infrastructure with foraging on the ground (P. Diniz pers. obs.). 'Foraging' was recorded when the bird was on the ground and includes periods of 'head-up' vigilance (Fernández-Juricic *et al.* 2004). Rufous Horneros usually perch high on trees or human infrastructures, allowing them to detect territorial intruders (Diniz *et al.* 2020). Here we considered this behaviour as sentinel activity, which probably includes territorial sentinel behaviour (Walker *et al.* 2016) and predator detection (Bednekoff 2015), though it may also include other forms of social monitoring, preening, resting and singing. 'Nest-building' (when the parental bird was collecting nest material or building its nest) and 'parental care' (when the parental bird was caring for offspring inside the nest) were not considered further in our analyses because they represented only 9% of the valid scans ($n = 17\ 604$).

Vocal behaviour

Song data were retrieved from previous studies (Diniz *et al.* 2018, 2019), except for the acoustic parameters of co-ordinated songs. Briefly, we recorded songs of focal adults using a Marantz PMD 660 recorder (settings: WAVE format, sampling rate = 48 or 44.1 kHz, resolution = 16 or 24 bits) and a Sennheiser ME66 (frequency response = 0.04–20 kHz) or Yoga HT-81

microphone (frequency response = 0.04–16 kHz) during each 1-h focal session (Diniz *et al.* 2018). We demarcated the start and end of each solo song and each contribution in duets or chorus by males and females using the waveform and the spectrogram in Raven Pro 1.5. We ignored the rarer songs of juveniles (see Diniz *et al.* 2018 for more details).

For each focal adult bird and in each 1-h recording, we measured the following variables: song initiation (number of initiated songs: solo songs plus initiated duets or choruses); song answering rate (proportion of songs initiated by the partner that were answered by the focal individual, thus creating a duet or chorus); phrase duration (duration of the contribution of each sex) in co-ordinated songs (i.e. duets and choruses; mean $\pm$ sd = 44.83 $\pm$ 11.44 co-ordinated songs per social unit, $n = 538$ songs); and acoustic parameters of duets.

We standardized the sampling rate (44.1 kHz) and the resolution (16 bits) of the recordings in Adobe Audition 8.0.0 before measuring the acoustic properties of duets. We selected only high-quality duets (high signal-to-noise ratio) that were not emitted during chases with intruding birds. We analysed duets produced by partners that sang close (~ < 10 m) to each other as indicated by the relative amplitude of male and female contributions on the oscillogram. This procedure minimizes amplitude bias favouring the nearer of the duetting partners.

We estimated minimum and maximum frequencies using the threshold method (Podos 1997, Ríos-Chelén *et al.* 2016, 2017), considering an amplitude threshold of –15 dBA relative to the peak frequency (settings, window: blackman, window length: 1024, overlap: 50, smooth: 1). This represents a conservative threshold to estimate the minimum frequency that includes most of the song while excluding peaks of low-frequency background noise in our duet samples (Ríos-Chelén *et al.* 2017). We smoothed the frequency spectrum to avoid biased estimations of minimum and maximum frequencies due to energy peaks across frequencies (Araya-Salas & Smith-Vidaurre 2017). Before estimating minimum and maximum frequencies, we filtered out frequencies < 500 Hz and > 10 kHz from all the recordings to reduce background noise (Diniz *et al.* 2020) and to eliminate frequency ranges that did not contain Rufous Hornero songs (Laje & Mindlin 2003). We

Table 1. Principal component analysis for acoustic measurements of duets by Rufous Hornero pairs ($n = 205$ duets, 12 pairs). We show loadings (values $\geq |0.6|$ are highlighted (bold)), eigenvalues and cumulative variance explained for the two principal component scores.

Acoustic parameter	PC1	PC2
Minimum frequency	**−0.87**	0.42
Maximum frequency	**0.62**	**0.77**
Frequency bandwidth	**0.89**	0.41
Mean frequency	0.02	**0.98**
Spectrographic entropy	**0.72**	0.30
Eigenvalues	2.44	1.98
Cumulative variance explained (%)	49	88

Measurements are as described in Araya-Salas and Smith-Vidaurre (2017). Minimum frequency and maximum frequency were estimated by the amplitude threshold method (see Methods: Vocal Behaviour for details). Frequency bandwidth: frequency range or difference between maximum frequency and minimum frequency. Mean frequency: mean frequency weighted by amplitude within the computed frequency range. Spectrographic entropy: product of energy distribution of the frequency spectrum and time envelope.

measured a total of five acoustic parameters (minimum frequency, maximum frequency, mean frequency, bandwidth and spectrographic entropy) for the high-quality duets (mean ± sd = 17.08 ± 5.38 per social unit; range = 8–26, $n = 205$ duets; Table 1) within the frequency range computed above and using the same settings as above except that here we did not use the frequency smoothing feature. All acoustic measurements were taken using the *warbleR* package in R (Araya-Salas & Smith-Vidaurre 2017).

We performed a principal component analysis (PCA, correlation matrix, varimax rotation) to reduce the dimensionality of our acoustic parameters and retained two principal component scores (PCs) with eigenvalues > 1 (Kaiser criteria; Kaiser 1960). The selected PCs explained 88% of the variance of the original acoustic variables (Table 1). We used these scores as our final acoustic variables in the statistical analyses. Additional details about song data sampling and analyses can be accessed in Diniz *et al.* (2018).

Statistical analyses

We analysed our data with generalized linear mixed models (GLMMs, package *glmmTMB*, Brooks *et al.* 2017) in R 4.0.0 (R Core Team 2020). The family of error distribution varied depending on the type of the response variable (continuous: Gaussian, count: Poisson, overdispersed count: negative binomial, binary or proportion: Binomial, overdispersed proportion: beta-binomial) (Zuur *et al.* 2009, Brooks *et al.* 2017, Douma & Weedon 2019). For each binomial and beta-binomial model, we chose the link function (*logit*, *probit* or *cloglog*) that produced the model with lowest Akaike's information criterion (AIC). Model residuals and assumptions were checked through the visualization of residuals plots and using the packages *performance* (Lüdecke *et al.* 2020) and *DHARMa* (Hartig 2020).

To validate our human activity classification, we analysed the effect of human activity level (fixed effect) on each of the number of pedestrians, the number of vehicles and noise (LAeq). The time of day (in decimal hours, *ln*-transformed) related to each sampling of human activity was added as a covariate, fixed effect, and the territory identity as a random effect in each model. We also analysed the estimated number of cars for each parking lot as a function of human activity level (fixed effect) and parking lot (random effect) using a zero-inflation model.

Human activities may affect females and males differently (Ellenberg *et al.* 2009, Guay *et al.* 2013, Tablado & Jenni 2017) and Rufous Hornero sexes differ in the expression of vocal behavioural traits (e.g. song initiation and duration, song answering) and their variation relative to breeding phenology (Diniz *et al.* 2018). Consequently, we analysed the effect of human activity level on the behaviour of each sex in separate models whenever possible. First, we analysed the effect of human activity level on the proportion of time spent in sentinel and foraging behaviour for each sex separately. For example, for foraging behaviour we measured the proportion of time a bird spent foraging in each observation session (i.e. number of scans in which the bird was foraging/total scans in which the bird was tracked). We included human activity level as a fixed effect in the models. Breeding phenology is well known to affect foraging effort in birds (e.g. Weathers & Sullivan 1993) and was added as a categorical effect in the models (Supporting Information Table S1). Breeding phenology was classified in three stages: pre-breeding stage (non-breeding season prior to breeding), breeding stage (from fertile female period to fledging) and post-breeding stage (care of juveniles and beginning of the non-breeding

season) (adapted from Diniz *et al.* 2018). We accounted for repeat measures of individual birds by adding individual identity as a random factor in the models (Harrison *et al.* 2018) (Table 2).

We analysed the effect of human activity level on the following song traits (one model for each variable): song initiation and song answering (sexes analysed separately), phrase duration in co-ordinated songs, and acoustic parameters of duets (the two PCs). We included human activity level and breeding phenology as fixed, categorical effects in the models. Song traits in the Rufous Hornero have also been shown to vary hourly (Diniz *et al.* 2018) and therefore we also included the time of day of vocal behaviour as a covariate. We added bird identity (song initiation and song answering) or observation session nested within pair identity (phrase duration in co-ordinated songs and acoustic parameters of duets) as random factors in the models (Table 2).

We used Type II Wald chi-square tests (*Anova* function, *car* package; Fox & Weisberg 2019), standardized model coefficients (β) and estimated marginal means (i.e. model predicted values, *ggeffect* function, *ggeffects* package; Lüdecke 2018) to evaluate the significance of predictor variables. We used pseudo, marginal r^2 (Nakagawa & Schielzeth 2013) to estimate the effect sizes for a version of each model containing only human activity levels as a fixed effect. The function *ggeffect* computes the marginal means while holding constant the continuous covariates and using the average proportion for categorical predictors (Lüdecke 2018). When we found a significant effect of human activity levels on any acoustic PC score, we repeated the models, replacing the PC with each original acoustic variable that was highly correlated with this PC (loadings ≥ |0.6|). In this latter case, *P*-values were adjusted for false discovery rates according to Benjamini and Hochberg (1995).

Table 2. Results of generalized linear mixed models to test for effects of human activity levels (i.e. weekends vs. weekdays) on sentinel, foraging and vocal behaviours in the Rufous Hornero.

Response variable	Family function	Sex or pair	Wald test χ^2 (*P*), (df = 1)	β ± se	Estimated marginal means (95% confidence interval (CI))	
					Weekends	Weekdays
Sentinel behaviour[1]	Beta-binomial[3]	Female	2.20 (0.14)	−0.16 ± 0.11	29 (25–34)[%]	33 (29–39)[%]
	Beta-binomial[3]	Male	2.26 (0.13)	−0.16 ± 0.11	33 (28–38)[%]	37 (32–43)[%]
Foraging[1]	Beta-binomial[4]	Female	0.60 (0.44)	0.07 ± 0.08	57 (51–63)[%]	55 (48–61)[%]
	Beta-binomial[3]	Male	2.53 (0.11)	0.14 ± 0.09	59 (54–64)[%]	54 (48–60)[%]
Song initiation[1]	Negative binomial 1	Female	0.62 (0.43)	−0.11 ± 0.14	1.58 (1.31–1.92)	1.77 (1.43–2.18)
	Negative binomial 2	Male	0.82 (0.37)	−0.10 ± 0.11	3.23 (2.57–4.05)	3.55 (2.80–4.52)
Song answering[1]	Binomial[4]	Female	0.05 (0.81)	0.03 ± 0.11	60 (50–69)[%]	59 (49–68)[%]
	Binomial[5]	Male	0.30 (0.58)	0.15 ± 0.27	73 (65–80)[%]	70 (61–78)[%]
Phrase duration[2]	Gaussian	Female	0.10 (0.75)	0.03 ± 0.10	5.46 (5.19–5.74) s	5.41 (5.11–5.71) s
	Gaussian	Male	0.58 (0.45)	−0.08 ± 0.11	6.28 (5.91–6.66) s	6.43 (6.03–6.83) s
Acoustic features (PC1)[2]	Gaussian	Pair	0.21 (0.65)	0.05 ± 0.11	0.33 (−0.68 to 1.35)	0.21 (−0.85 to 1.27)
Acoustic features (PC2)[2]	Gaussian	Pair	**3.87 (0.049)**	0.23 ± 0.12	0.38 (−0.41 to 1.16)	−0.11 (−0.93 to 0.72)

We show results of Type II Wald chi-square tests (and *P*-values), model coefficients and estimated marginal means. See results of Type II Wald tests for covariates and descriptive statistics for the response variables in Supporting Information Tables S1 and S3, respectively. Model reference level: weekday. Significant results are shown in bold. Sentinel behaviour: proportion of time spent perched in territorial vigilance. Foraging: proportion of time spent foraging on the ground. Song initiation: number of initiated songs (solos plus initiated duets). Song answering: proportion of songs initiated by the partner that were answered by the focal individual creating a duet or chorus. Phrase duration: duration of an individual contribution in duets or choruses (in seconds). Acoustic features: acoustic parameters of duets between pair members. Models may include [1]individual ID or [2]observation session ID nested within individual ID as random terms. Link function: [3]*cloglog*, [4]*probit*, [5]*logit*. [%] percentage of time spent in each behaviour or percentage of songs initiated by the partner and answered by the focal individual.

RESULTS

Human activity levels were higher on weekdays

Human activity levels (high on weekdays vs. low on weekends) reflected human activity types at each territory (number of pedestrians and cyclists, number of vehicles and ambient noise) and the main parking lots on campus (number of vehicles). The number of pedestrians and cyclists (Poisson GLMM, $\chi^2 = 21.40$, $P < 0.001$; $\beta \pm se = 2.79 \pm 0.59$; $r^2 = 76\%$), number of vehicles (ln+1-transformed, Gaussian GLMM, $\chi^2 = 8.90$, $P = 0.003$; $\beta \pm se = 0.18 \pm 0.16$; $r^2 = 25\%$) and ambient noise (Gaussian GLMM, $\chi^2 = 9.66$, $P = 0.002$; $\beta \pm se = 1.28 \pm 0.52$; $r^2 = 38\%$) were higher on weekdays than on weekends (Fig. 1, Supporting Information Table S2), irrespective of time of day (Type II Wald chi-square tests, $P > 0.13$) and across territories. The number of parked vehicles was also higher on weekdays than on weekends across three of the main parking lots on campus ($\chi^2 = 436.28$, $P < 0.001$; $\beta \pm se = 1.52 \pm 0.07$; $r^2 = 54\%$) (Supporting Information Fig. S3).

Sentinel and foraging behaviours were similar on weekends and on weekdays

We found no significant difference in the proportion of time that either sex spent as sentinels between weekdays (estimated marginal means, females: 33%, males: 37%) and weekends (females: 29%; males: 33%; Fig. 2, Table 2). The effect sizes for these differences were small ($r^2 < 0.4\%$) and inaccurate, as the confidence intervals for the estimated marginal means overlapped between weekdays and weekends for both sexes (Table 2). Similarly, we found no significant difference in the proportion of time that either sex spent foraging between weekdays (estimated marginal means, females: 55%, males: 54%) and weekends (females: 57%, males: 59%; Fig. 2, Table 2). The effect sizes for these differences were small ($r^2 < 0.9\%$) and inaccurate (Table 2; see also Supporting Information Tables S1, S3 and S4).

Vocal behaviour varied little with human activity levels

For both sexes, song initiation rate, song answering and phrase duration in co-ordinated songs did not vary between weekdays and weekends ($r^2 < 0.04\%$, Table 2, Fig. 3). The acoustic parameters of duets varied significantly with human activity levels when considering one of the two PC scores (PC2, Fig. 3). However, the effect size of this relationship was small ($r^2 < 1.9\%$) and inaccurate, as there was a large overlap of confidence intervals for marginal means between weekdays and weekends (Table 2).

The analysis of the original acoustic variables that were most correlated (loadings $> |0.6|$) with PC2 did not indicate a significant difference in the mean and minimum frequencies of duets between weekdays and weekends. Although Rufous Horneros seemingly sang duets with higher maximum
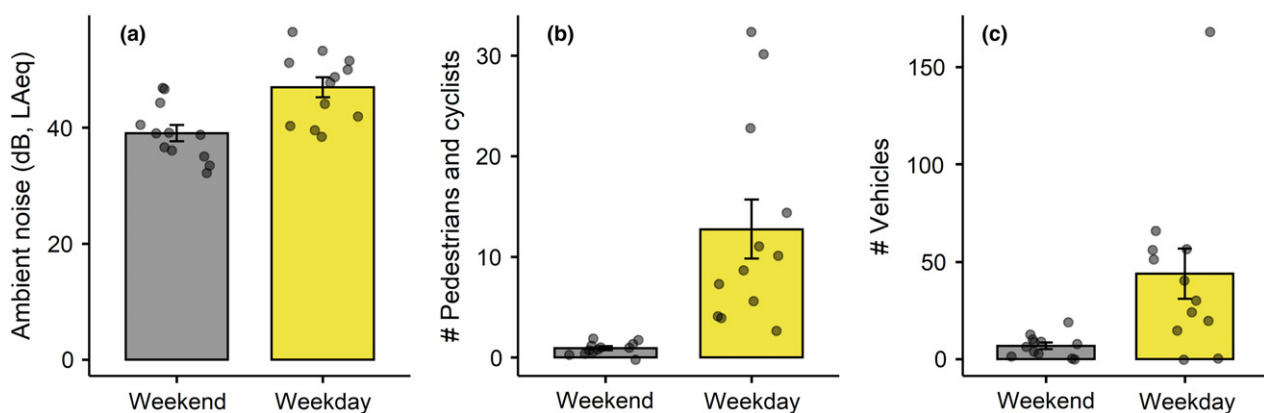

Figure 1. Variation in ambient noise (a), number of pedestrians and cyclists (b), and traffic flow (c) between weekends and weekdays. The measurements were taken for 5-min periods both on a weekend day and on a weekday at each territory. Mean ± se. Samples are shown by grey dots. n = 12 Rufous Hornero territories. [Colour figure can be viewed at wileyonlinelibrary.com]
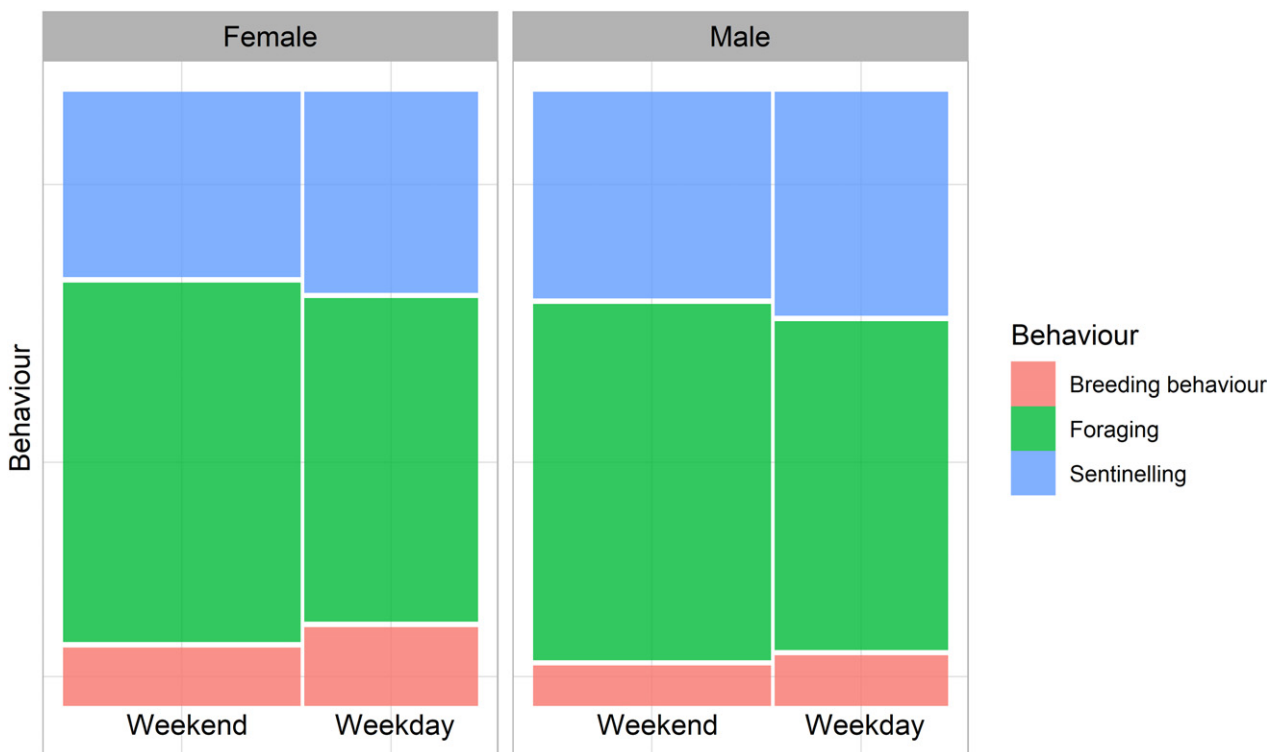
Figure 2. Time-budget for different behaviours of the Rufous Hornero as a function of temporal variation in human activity levels (weekend vs. weekdays). The *y*-axis represents the proportion of scan samples where each adult bird was performing each behaviour. Data from different focal sessions (*n* = 161), pairs (*n* = 12) and individuals (*n* = 24), as well as data from 'Nest-building' and 'Parental care', were pooled for illustration purposes (*n* = 17 604 scans). The width of the bars represents the relative sample size differences (weekend: *n* = 10 177 scans in 93 sessions; weekdays: *n* = 7427 scans in 68 sessions). [Colour figure can be viewed at wileyonlinelibrary.com]

frequency (~ 80 Hz, Table 3) during weekends than on weekdays, this relationship had a small and inaccurate effect size (r^2 = 1.6%, Table 3), it was not statistically significant after accounting for multiple tests, and it did not result in increased values of frequency bandwidth (β ± se: 0.12 ± 0.11).

DISCUSSION

Overall, our results provide little support for the weekend effect hypothesis, which predicts that non-human animals should behave differently on weekends than on weekdays, by matching the weekly cycles of human activity levels (Stalmaster & Kaiser 1998). Despite higher human activity levels during weekdays, we show that a diverse array of behaviours (sentinel behaviour, foraging effort, singing effort, duet responsiveness, song length and acoustic parameters of duets) were

similarly expressed by the Rufous Hornero on weekdays and on weekends.

We acknowledge that our study has two limitations. First, we sampled few Rufous Hornero pairs (*n* = 12); however, for each subject we have a high power to detect behavioural differences between weekends and weekdays, considering the high sampling effort (weekends: *n* = 93 sessions; weekdays: *n* = 68 sessions) across the studied pairs (Table S4). Second, we cannot discard the possibility that the low levels of human activity on weekends might still have been sufficient to disturb the Rufous Horneros and trigger behavioural adjustments. Nonetheless, we expected some variation in bird behaviour between weekends and weekdays considering that the level of human activity was on average up to 14 times greater on weekdays than on weekends (number of pedestrians and cyclists, Table S2).
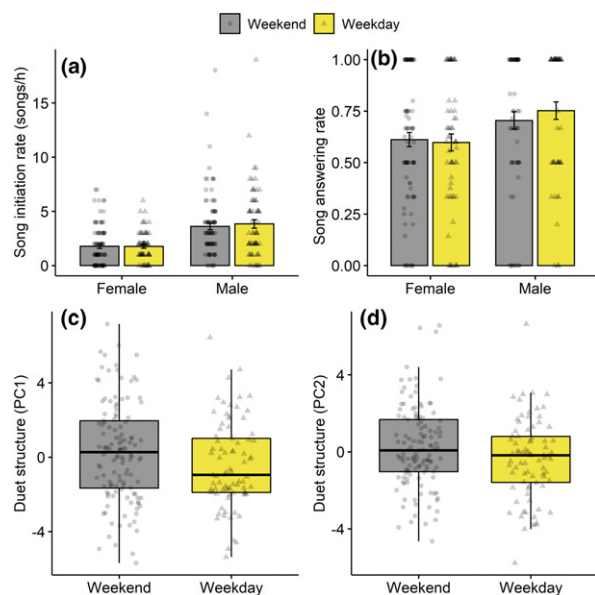
Figure 3. Vocal behaviour and acoustic structure of duets (2 PC scores) as a function of temporal variation in human activity levels (weekend vs. weekdays). Song initiation rate (a) is number of solos plus initiated duets. Song answering rate (b) is the proportion of songs initiated by the partners that were answered by the focal individual. High values of PC1 (c) mean broadband duets with high maximum frequency and entropy, and low minimum frequency. High values of PC2 (d) mean high-pitch duets with high maximum frequency. (a,b) Mean ± se across focal sessions. (c,d) Boxplot with median, quartiles, minimum and maximum values. Data from different groups were pooled for illustration purposes. Samples represented by the number of focal sessions (a,b) and duets (c,d) are shown by grey dots (weekends) and triangles (weekdays). Sample sizes are given in Supporting Information Table S4. [Colour figure can be viewed at wileyonlinelibrary.com]

Sentinel and foraging behaviours

We expected that birds would be more vigilant (territorial sentinel behaviour) and forage less on weekdays than on weekends due to higher human activity during weekdays. Birds behaved as predicted, spending slightly more time (~ 4%) as sentinels and less time (~ 2–5%) foraging on weekdays. In accordance with our models, these results mean that birds spend on average ~ 29 more minutes as sentinels and ~ 14–36 fewer minutes foraging per day on weekdays than on weekends (assuming 12 daylight hours per day). However, the results were not statistically significant, the effect sizes were small and model-predicted values had a high degree of uncertainty (Table 2). Our results indicate that the Rufous Hornero tolerates large temporal variation in human activity levels that include traffic, noise and human presence. Alternatively, our results may suggest that the low levels of human activity on weekends are already sufficient to disturb the birds and trigger behavioural adjustments in the Rufous Hornero.

The Rufous Hornero is one of the most common bird species in urban and other human-modified habitat types within its distribution range (e.g. Fontana *et al.* 2011). Birds from a southern population of this species did not change their foraging rate (pecking rate) in response to human approach but became alert when foraging on the ground and escaped more quickly in response to human approach in the context of decreasing human density (Prestes *et al.* 2018). Human activity therefore seems to be associated with escape behaviour but is weakly associated with territorial sentinel behaviour or foraging rate and effort in this species.

The weekend effect of animal tolerance to human activity may be more pronounced in rural areas, where baseline human activity levels are lower compared with urban areas (Pelletier 2006, Tarjuelo *et al.* 2015, Vincze *et al.* 2016, Nix *et al.*

Table 3. Results of generalized linear mixed models to test for effects of human activity levels (i.e. weekends vs. weekdays) on acoustic parameters of duets that mostly contributed to PC2 (see Table 1).

Response variable	Family function	Wald test χ^2 (*P*), df = 1	B ± se	Estimated marginal means (kHz, 95% CI)	
				Weekends	Weekdays
Mean frequency	Gaussian	2.77 (0.10)	0.20 ± 0.12	3.15 (3.09–3.21)	3.12 (3.06–3.18)
Maximum frequency	Gaussian	4.02 (0.045*)	0.23 ± 0.12	4.01 (3.89–4.14)	3.93 (3.80–4.07)

We show results of Type II Wald chi-square tests (and *P*-values), model coefficients and estimated marginal means (predicted values). Breeding phenology and time of day were also included as fixed effects in the models (results not shown). See descriptive statistics for the response variables in Supporting Information Table S3. Model reference level: weekday. Models include observation session ID nested within individual ID as random terms. *P*-value no longer significant after controlling for false discovery rates.

2018). Results comparable to ours were found for the Red-winged Starling *Onychognathus morio*, another common urban bird inhabiting university campuses, which had similar time-budgets on weekends and on weekdays (Stofberg *et al.* 2019). Nevertheless, further studies with presumably less tolerant urban animals (e.g. larger animals, Blumstein 2006) and other behavioural traits (e.g. escape decision, Cavalli *et al.* 2016) are needed to understand fully the behavioural response of urban animals to temporal variation in human activity levels.

Vocal behaviour

Noise was higher on weekdays than on weekends (Fig. 1). We predicted that birds would sing at higher rates and produce longer, tonal and higher pitched songs on weekdays, assuming these traits would increase signal redundancy and reduce signal masking by noise, thus minimizing the hampering effects of noise on signal transmission (Lohr *et al.* 2003, Halfwerk *et al.* 2011a, Gil & Brumm 2014, Shannon *et al.* 2016). In this context, our results weakly supported the weekend effect hypothesis. Singing effort and song length did not vary significantly relative to the weekly cycles in human activity, suggesting that birds did not increase signal redundancy as human activity levels increased. Unexpectedly, birds emitted duets with slightly higher maximum frequency (~ 80 Hz) on weekends than on weekdays (Mendes *et al.* 2011, 2017), whereas minimum frequency was unrelated to weekly cycles of human activity levels.

We suggest that changes in the physical obstacles or barriers to sound propagation, and not noise, are more probable explanations for the slightly lower pitched Rufous Hornero duets on weekdays. A previous study showed that the frequency structure of songs among territorial pairs is not correlated with spatial variation in noise in two urban populations of the Rufous Hornero (Ríos-Chelén *et al.* 2012). In addition, Rufous Hornero occupancy is higher in airport than in control areas (Alquezar *et al.* 2020), suggesting that this species may tolerate high levels of anthropogenic noise. Hence, the Rufous Hornero may not adjust vocal behaviour or song structure to counteract urban, spatiotemporal variation in anthropogenic noise. However, we cannot exclude the possibility that Rufous Horneros might adjust song amplitude and the usage of syllable types to

cope with periodic changes in anthropogenic noise (Zollinger *et al.* 2012, Walters *et al.* 2019).

The impervious surfaces and barriers (e.g. buildings) in the urban environment can scatter, absorb or reflect high-frequency sounds (Wiley & Richards 1982), potentially creating reverberations (Slabbekoorn *et al.* 2007) and distorting some parts of the signal (Dowling *et al.* 2012). The numbers of barriers and surfaces (e.g. vehicles) that absorb or reverberate signals increases on weekdays (Figs 1 and S3), favouring vocal adjustments to emit low-frequency sounds on weekdays relative to weekends (Dowling *et al.* 2012). Similarly, low-pitched whistles are best transmitted in urban areas and are more likely to be produced by urban than rural White-crowned Sparrows *Zonotrichia leucophrys* (Phillips *et al.* 2020). Nevertheless, the small increase in maximum frequency of Rufous Hornero duets (~ 80 Hz) on weekends may only marginally improve signal transmission (Francis *et al.* 2011).

Given the small and inconclusive effects of weekly cycles of human activity levels on the acoustic parameters of Rufous Hornero duets, we consider that our results do not provide evidence of vocal plasticity in terms of frequency and song length shifts in response to human activity levels. Vocal learning is neuro-anatomically constrained in tracheophone suboscine passerines (Doupe & Kuhl 1999, Tobias *et al.* 2012, Liu *et al.* 2013), which might limit vocal plasticity and vocal adjustment to anthropogenic noise (Ríos-Chelén *et al.* 2012, 2018, Gentry *et al.* 2017). A few other studies showed weak or no song flexibility in response to human activities in suboscine passerines (Francis *et al.* 2011, Ríos-Chelén *et al.* 2018, but see Gentry *et al.* 2017). In contrast, it has been shown that oscines are more capable than suboscines of adjusting acoustic signals in noisy conditions (Ríos-Chelén *et al.* 2012). We therefore encourage further studies to test the weekend effect hypothesis in both oscine and suboscine passerines.

Duetting responsiveness

We suggested that noise could mask a song initiated by one bird and prevent the response of the partner bird. However, our results do not support the idea that duetting species may be particularly vulnerable to anthropogenic noise. Song answering rate (song responsiveness to partner's songs) did

not vary with human activity levels, suggesting that duetting behaviour is not associated with weekly cycles of human activity levels. Rufous Horneros emit loud duets (~ 92 dBA at 1 m) that appear to suffer little from signal attenuation across short distances (Zollinger & Brumm 2015) and partners often duet when they are close to each other (Diniz *et al.* 2020), which might prevent noise from hampering communication between duetters. Anthropogenic noise is therefore most likely to interfere in the communication between duetters in species that produce quiet or low-frequency duets or in which partners duet at a distance.

Conclusion

Overall, our results provide little support for the weekend effect hypothesis, and suggest that the Rufous Hornero is either habituated or indifferent to periodic changes in human activity levels. The absence of significant behavioural responses to weekly cycles in human activity levels may reflect a high degree of tolerance of human activity by Rufous Horneros that allows the species to occupy urban environments successfully. Further studies could explore whether Rufous Hornero juveniles are insensitive or become habituated to human presence during their long stay in the natal territory (Fraga 1980).

AUTHOR CONTRIBUTIONS

Pedro Diniz: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (equal); Methodology (lead); Resources (supporting); Visualization (lead); Writing-original draft (lead). **Edvaldo Ferreira Silva Júnior:** Conceptualization (supporting); Data curation (supporting); Investigation (equal); Methodology (supporting); Writing-review & editing (supporting). **Regina Helena Macedo:** Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Resources (lead); Supervision (lead); Writing-review & editing (lead).

CONFLICT OF INTERESTS

The authors declare that they have no conflicts of interest.

ETHICS STATEMENT

This study was approved by the Brazilian environmental agency Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (ICMBio, licence number 45177-1). All procedures were performed in accordance with the Guidelines to the Use of Wild Birds in Research of the Ornithological Council (Fair *et al.* 2010). The researchers recorded the behaviour and vocalizations while keeping a distance of > 10 m from the birds. No bird behaved abnormally in the presence of the researchers or abandoned its nest or territory due to researcher disturbance.

Data Availability Statement

All data and codes that support the findings of this study are fully avaiable on Mendeley Data (Diniz et al. 2021).

REFERENCES

Alquezar, R.D., Tolesano-Pascoli, G., Gil, D. & Macedo, R.H. 2020. Avian biotic homogenization driven by airport-affected environments. *Urban Ecosyst.* 23: 507–517.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.

Araya-Salas, M. & Smith-Vidaurre, G. 2017. warbleR: an R package to streamline analysis of animal acoustic signals. *Methods Ecol. Evol.* 8: 184–191.

Aruwajoye, A.O. 2016. *Previsão da demanda de transporte no campus Darcy Ribeiro da Universidade de Brasília. Bachelor Thesis in Civil and Environmental Engineering.* Universidade de Brasília.

Bautista, L.M., García, J.T., Calmaestra, R.G., Palacín, C., Martín, C.A., Morales, M.B., Bonal, R. & Viñuela, J. 2004. Effect of weekend road traffic on the use of space by raptors. *Conserv. Biol.* 18: 726–732.

Beale, C.M. & Monaghan, P. 2004. Human disturbance: People as predation-free predators? *J. Appl. Ecol.* **41**: 335–343.

Bednekoff, P.A. 2015. Sentinel behavior: a review and prospectus. In Naguib, M.. (eds) *Advances in the Study of Behavior*. 47th edn. 115–145. New York, NY: Academic Press.

Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B* **57**: 289–300.

Blumstein, D.T. 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim. Behav.* **71**: 389–399.

Blumstein, D.T., Geffroy, B., Samia, D.S.M. & Bessa, E. 2017. In *Ecotourism's Promise and Peril: A Biological Evaluation*. New York, NY: Springer.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M. & Bolker, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**: 378.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* **73**: 434–440.

Brumm, H. & Slater, P.J.B. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behav. Ecol. Sociobiol.* **60**: 475–481.

Campos, D.P., Bander, L.A., Raksi, A. & Blumstein, D.T. 2009. Perch exposure and predation risk: a comparative study in passerines. *Acta Ethol.* **12**: 93–98.

Casas, F., Benítez-López, A., Tarjuelo, R., Barja, I., Viñuela, J., García, J.T., Morales, M.B. & Mougeot, F. 2016. Changes in behaviour and faecal glucocorticoid levels in response to increased human activities during weekends in the Pin-tailed Sandgrouse. *Sci. Nat.* **103**: 91.

Catchpole, C.K. & Slater, P.J.B. 2008. *Bird song: Biological Themes and Variations*. , 2nd edn. New York: Cambridge University Press.

Cavalli, M., Isacch, J.P., Baladrón, A.V., Biondi, L.M. & Bó, M.S. 2016. Differing nest-defence behaviour in urban and rural populations of breeding Burrowing Owls. *Emu* **116**: 428–434.

Cerveny, R.S. & Balling, R.C. 1998. Weekly cycles of air pollutants, precipitation and tropical cyclones in the coastal NW Atlantic region. *Nature* **394**: 561–563.

Diaz, M., Parra, A., Gallardo, C., Díaz, M., Parra, A. & Gallardo, C. 2011. Serins respond to anthropogenic noise by increasing vocal activity. *Behav. Ecol.* **22**: 332–336.

Diniz, P., da Silva, E.F., Webster, M.S. & Macedo, R.H. 2018. Duetting behavior in a Neotropical ovenbird: sexual and seasonal variation and adaptive signaling functions. *J. Avian Biol.* **49**: jav-01637.

Diniz, P., Macedo, R.H. & Webster, M.S. 2019. Duetting correlates with territory quality and reproductive success in a suboscine bird with low extra-pair paternity. *Auk* **136**: 1–13.

Diniz, P., Rech, G.S., Ribeiro, P.H.L.L., Webster, M.S. & Macedo, R.H. 2020. Partners coordinate territorial defense against simulated intruders in a duetting ovenbird. *Ecol. Evol.* **10**: 81–92.

Diniz, P., Ribeiro, P.H.L., Rech, G.S. & Macedo, R.H. 2016. Monochromatism, cryptic sexual dimorphism and lack of assortative mating in the Rufous Hornero, *Furnarius rufus albogularis*. *Emu* **116**: 294–300.

Diniz, P., Silva-Jr, E.F. & Macedo, R.H. (2021) Data from: Urban cycles of human activity do not significantly alter the behaviour of a duetting bird. *Mendeley Data.* **V1**. https://doi.org/10.17632/zjpgt49yrf.1

Douma, J.C. & Weedon, J.T. 2019. Analysing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. *Methods Ecol. Evol.* **10**: 1412–1430.

Doupe, A.J. & Kuhl, P.K. 1999. Birdsong and human speech: common themes and mechanisms. *Annu. Rev. Neurosci.* **22**: 567–631.

Dowling, J.L., Luther, D.A. & Marra, P.P. 2012. Comparative effects of urban development and anthropogenic noise on bird songs. *Behav. Ecol.* **23**: 201–209.

Ellenberg, U., Mattern, T. & Seddon, P.J. 2009. Habituation potential of Yellow-eyed Penguins depends on sex, character and previous experience with humans. *Anim. Behav.* **77**: 289–296.

Fair, J., Paul, E. & Jones, J. (2010) *Guidelines to the Use of Wild birds in Research*. Washington, DC: Ornithological Council.

Fernández-Juricic, E., Erichsen, J.T. & Kacelnik, A. 2004. Visual perception and social foraging in birds. *Trends Ecol. Evol.* **19**: 25–31.

Fernández-Juricic, E. & Tellería, J.L. 1999. Recruitment patterns of Blackbirds (*Turdus merula*) in urban fragmented populations. *Ardeola* **46**: 61–70.

Fernández-Juricic, E. & Tellería, J.L. 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study* **47**: 13–21.

Fokidis, H.B., Orchinik, M. & Deviche, P. 2011. Context-specific territorial behavior in urban birds: No evidence for involvement of testosterone or corticosterone. *Horm. Behav.* **59**: 133–143.

Fontana, C.S., Burger, M.I. & Magnusson, W.E. 2011. Bird diversity in a subtropical South-American City: effects of noise levels, arborisation and human population density. *Urban Ecosyst.* **14**: 341–360.

Fox, J. & Weisberg, S. 2019. *An R Companion to Applied Regression*. Thousand Oaks, CA: SAGE Publications.

Fraga, R.M. 1980. The breeding of Rufous Horneros (*Furnarius rufus*). *Condor* **82**: 58–68.

Francis, C.D., Ortega, C.P., Cruz, A., Soc, P.R., Francis, C.D. & Catherine, P. 2011. Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proc. Biol. Sci.* **278**: 2025–2031.

Frid, A. & Dill, L. 2002. Human-caused disturbanve stimuli as a form of predation risk. *Conserv. Ecol.* **6**: 16.

Gentry, K.E., McKenna, M.F. & Luther, D.A. 2017. Evidence of suboscine song plasticity in response to traffic noise fluctuations and temporary road closures. *Bioacoustics* **4622**: 1–17.

Gil, D. & Brumm, H. 2014. Acoustic communication in the urban environment: patterns, mechanisms, and potential consequences of avian song adjustments. In Gil, D. & Brumm, H. (eds) *Avian Urban Ecology*: 69–83. New York, NY: Oxford University Press.

Gross, K., Pasinelli, G. & Kunc, H.P. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. *Am. Nat.* **176**: 456–464.

Guay, P.-J., Lorenz, R.D.A., Robinson, R.W., Symonds, M.R.E. & Weston, M.A. 2013. Distance from water, sex and approach direction influence flight distances among habituated Black Swans. *Ethology* **119**: 552–558.

Gutzwiller, K.J. & Anderson, S.H. 1994. Effects of human intrusion on song occurrence and singing consistency in subalpine birds. *Auk* **111**: 28–37.

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C. & Slabbekoorn, H. 2011a. Low-frequency songs lose their potency in noisy urban conditions. *Proc. Natl Acad. Sci. USA* **108**: 14549–14554.

Halfwerk, W., Holleman, L.J.M., Lessells, C.M. & Slabbekoorn, H. 2011b. Negative impact of traffic noise on avian reproductive success. *J. Appl. Ecol.* **48**: 210–219.

Hanna, D., Blouin-Demers, G., Wilson, D.R. & Mennill, D.J. 2011. Anthropogenic noise affects song structure in Red-winged Blackbirds (*Agelaius phoeniceus*). *J. Exp. Biol.* **214**: 3549–3556.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J. & Inger, R. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* **6**: e4794.

Hartig, F. 2020. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.* R package version 0.3.3.0.

Kaiser, H.F. 1960. The application of eletronic computers to factor analysis. *Educ. Psychol. Meas.*, **20**: 141–151.

Lafferty, K.D. 2001. Birds at a Southern California beach: Seasonality, habitat use and disturbance by human activity. *Biodivers. Conserv.* **10**: 1949–1962.

Laje, R. & Mindlin, G. 2003. Highly structured duets in the song of the South American hornero. *Phys. Rev. Lett.* **91**: 1–4.

Liu, W., Wada, K., Jarvis, E.D. & Nottebohm, F. 2013. Rudimentary substrates for vocal learning in a suboscine. *Nat. Commun.* **4**: 2082.

Lohr, B., Wright, T.F. & Dooling, R.J. 2003. Detection and discrimination of natural calls in masking noise by birds: Estimating the active space of a signal. *Anim. Behav.* **65**: 763–777.

Lüdecke, D. 2018. *ggeffects*: Tidy data frames of marginal effects from regression models. *J. Open Source Software.* https://doi.org/10.21105/joss.00772.

Lüdecke, D., Makowski, D., Waggoner, P. & Patil, I. 2020. *Assessment of Regression Models Performance.* Available from: CRAN. https://easystats.github.io/performance/

Mendes, S., Colino-Rabanal, V.J. & Peris, S.J. 2011. Bird song variations along an urban gradient: the case of the European blackbird (*Turdus merula*). *Landsc. Urban Plan.* **99**: 51–57.

Mendes, S., Colino-Rabanal, V.J. & Peris, S.J. 2017. Adaptación acústica del canto de *Turdus leucomelas* (Passeriformes: Turdidae) a diferentes niveles de ruido antrópico, en el área metropolitana de Belém de Pará, Brasil. *Rev. Biol. Trop.* **65**: 633–642.

Mentesana, L., Moiron, M., Guedes, E., Cavalli, E., Tassino, B. & Adreani, N.M. 2020. Defending as a unit: sex- and context-specific territorial defence in a duetting bird. *Behav. Ecol. Sociobiol.* **74**: art. 111.

Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**: 133–142.

Nemeth, E. & Brumm, H. 2010. Birds and anthropogenic noise: Are urban songs adaptive? *Am. Nat.* **176**: 465–475.

Nix, J.H., Howell, R.G., Hall, L.K. & McMillan, B.R. 2018. The influence of periodic increases of human activity on crepuscular and nocturnal mammals: Testing the weekend effect. *Behav. Processes* **146**: 16–21.

Payne, N.L., van der Meulen, D.E., Suthers, I.M., Gray, C.A. & Taylor, M.D. 2014. Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing anthropogenic disturbance. *Mar. Biol.* **162**: 539–546.

Pelletier, F. 2006. Effects of tourist activities on ungulate behaviour in a mountain protected area. *J. Mt. Ecol.* **8**: 15–19.

Perona, A.M., Urios, V. & López-López, P. 2019. Holidays? Not for all. Eagles have larger home ranges on holidays as a consequence of human disturbance. *Biol. Conserv.* **231**: 59–66.

Phillips, J.N., Rochefort, C., Lipshutz, S., Derryberry, G.E., Luther, D. & Derryberry, E.P. 2020. Increased attenuation and reverberation are associated with lower maximum frequencies and narrow bandwidth of bird songs in cities. *J. Ornithol.* **161**: 593–608.

Podos, J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution (N.Y.)* **51**: 537–551.

Potvin, D.A. 2017. Coping with a changing soundscape: avoidance, adjustments and adaptations. *Anim. Cogn.* **20**: 9–18.

Prestes, T.V., Manica, L.T. & de Guaraldo, A. C. 2018. Behavioral responses of urban birds to human disturbance in urban parks at Curitiba, Paraná (Brazil). *Rev. Bras. Ornitol.* **26**: 77–81.

R Core Team 2020. *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Remsen Jr., V.J. & Bonan, A. 2020. Rufous Hornero (*Furnarius rufus*). In del del Hoyo, J., Elliot, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds) *Handbook of the Birds of the World Alive.* **version 1**. Ithaca, NY: Cornell Lab of Ornithology. https://doi.org/10.2173/bow.rufhor2.01

Ríos-Chelén, A.A., Cuatianquiz-Lima, C., Bautista, A. & Martínez-Gómez, M. 2018. No reliable evidence for immediate noise-induced song flexibility in a suboscine. *Urban Ecosyst.* **21**: 15–25.

Ríos-Chelén, A.A., Lee, G.C. & Patricelli, G.L. 2016. A comparison between two ways to measure minimum frequency and an experimental test of vocal plasticity in Red-winged Blackbirds in response to noise. *Behaviour* **153**: 1445–1472.

Ríos-Chelén, A.A., McDonald, A.N., Berger, A., Perry, A.C., Krakauer, A.H. & Patricelli, G.L. 2017. Do birds vocalize at higher pitch in noise, or is it a matter of measurement? *Behav. Ecol. Sociobiol.* **71**: 1–12.

Ríos-Chelén, A.A., Salaberria, C., Barbosa, I., Macías Garcia, C. & Gil, D. 2012. The learning advantage: bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. *J. Evol. Biol.* **25**: 2171–2180.

Roper, J.J. 2005. Sexually distinct songs in the duet of the sexually monomorphic Rufous Hornero. *J. Field Ornithol.* **76**: 234–236.

Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., McFarland, S. & Wittemyer, G. 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol. Rev.* **91**: 982–1005.

Sick, H. 2001. *Ornitologia Brasileira: uma introdução*. Rio de Janeiro: Nova Fronteira.

Silva, A.D., Samplonius, J.M., Schlicht, E., Valcu, M. & Kempenaers, B. 2014. Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. *Behav. Ecol.* **25**: 1037–1047.

Slabbekoorn, H., Yeh, P. & Hunt, K. 2007. Sound transmission and song divergence: a comparison of urban and forest acoustics. *Condor* **109**: 67–78.

Stalmaster, M.V. & Kaiser, J.L. 1998. Effects of recreational activity on wintering Bald Eagles. *Wildl. Monogr.* **137**: 3–60.

Stofberg, M., Cunningham, S.J., Sumasgutner, P. & Amar, A. 2019. Juggling a 'junk-food' diet: responses of an urban bird to fluctuating anthropogenic-food availability. *Urban Ecosyst.* **22**: 1019–1026.

Tablado, Z. & Jenni, L. 2017. Determinants of uncertainty in wildlife responses to human disturbance. *Biol. Rev.* **92**: 216–233.

Tarjuelo, R., Barja, I., Morales, M.B., Traba, J., Benítez-López, A., Casas, F., Arroyo, B., Delgado, M.P. & Mougeot, F. 2015. Effects of human activity on physiological and behavioral responses of an endangered steppe bird. *Behav. Ecol.* **26**: 828–838.

Tobias, J.A., Brawn, J.D., Brumfield, R.T., Derryberry, E.P., Kirschel, A.N.G. & Seddon, N. 2012. The importance of suboscine birds as study systems in ecology and evolution. *Ornitol. Neotrop.* **23**: 261–274.

Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V. & Liker, A. 2016. Habituation to human disturbance is faster in urban than rural House Sparrows. *Behav. Ecol.* **27**: 1304–1313.

Walker, L.A., York, J.E. & Young, A.J. 2016. Sexually selected sentinels? Evidence of a role for intrasexual competition in sentinel behavior. *Behav. Ecol.* **27**: 1461–1470.

Walters, M.J., Guralnick, R.P., Kleist, N.J. & Robinson, S.K. 2019. Urban background noise affects breeding song frequency and syllable-Type composition in the Northern Mockingbird. *Condor* **121**: duz002.

Wang, Y., Huang, Q., Lan, S., Zhang, Q. & Chen, S. 2015. Common Blackbirds *Turdus merula* use anthropogenic structures as nesting sites in an urbanized landscape. *Curr. Zool.* **61**: 435–443.

Weathers, W.W. & Sullivan, K.A. 1993. Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* **66**: 511–536.

Werneck, R.O. & de Arruda, F.S. 2017. Application of a methodology for the spatial analysis of air pollutant levels at the Darcy Ribeiro campus of the University of Brasília. *WIT Trans. Built Environ.* **176**: 351–360.

Wiley, R.H. & Richards, D.G. 1982. Sound transmission and signal detection. In Kroodsma, D.E. & Miller, E.H. (eds) *Acoustic Communication in Birds*: 131–181. New York, NY: Academic Press.

Williams, B.M., Durvasula, P.K. & Brown, D.E. 1998. Urban freeway traffic flow prediction application of seasonal autoregressive integrated moving average and exponential smoothing models. *Transport. Res. Rec.* **1644**: 132–141.

Wu, L., Zhi, Y., Sui, Z. & Liu, Y. 2014. Intra-urban human mobility and activity transition: evidence from social media check-in data. *PLoS One* **9**: e97010.

Zollinger, S.A. & Brumm, H. 2015. Why birds sing loud songs and why they sometimes don't. *Anim. Behav.* **105**: 289–295.

Zollinger, S.A., Podos, J., Nemeth, E., Goller, F. & Brumm, H. 2012. On the relationship between, and measurement of, amplitude and frequency in birdsong. *Anim. Behav.* **84**: e1–e9.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Territorial boundaries of the 12 social units of Rufous Horneros highlighted in satellite images from GOOGLE EARTH. The images are from the year we collected data on vocal, sentinel and foraging behaviours (2015) and from the year we sampled human activity levels (2017).

Appendix S2. Table S1. Results of generalized linear mixed models to test for effects of human activity levels (i.e. weekends vs. weekdays) on sentinel, foraging and vocal behaviours in the Rufous Hornero. We show results of Type II Wald chi-square tests (and P-values). n = number of trials (sentinel behaviour, foraging, song initiation and answering), co-ordinated songs (phrase duration) or duets (acoustic features). Significant results in bold.

Table S2. Human activities sampled for 5-min periods throughout the day (07:41–16:42 h) at weekends (low human activity) and on weekdays (high human activity) in Rufous Hornero territories (*n* = 12) at the Universidade de Brasília campus, central Brazil. Mean ± se.

Table S3. Average values of sentinel, foraging and vocal behaviours in the Rufous Hornero across varying human activity levels (i.e. weekends vs.

weekdays). n = number of trials (sentinel behaviour, foraging, song initiation and answering), co-ordinated songs (phrase duration) or duets (acoustic features).

Table S4. Sample sizes for global models and standard deviation for random factors in the final models.

Figure S1. Human population in the campus Darcy Ribeiro of the Universidade de Brasília, Brazil. Campus population size comprises the sum of the numbers of students, professors and technicians. Behavioural observations of birds were undertaken in 2015 (human population size: 51 908) and measurements of human activity in 2017 (human population size: 53 657) (highlighted in red). Retrieved on 10 July 2020, from http://www.dpo.unb.br

Figure S2. Three of the main parking lots at Universidade de Brasília: Pavilhão Anísio Teixeira and Pavilhão João Calmon (PAT-PJC, red), ICC Norte (blue), and ICC Sul (yellow). Photo taken on 11 June 2015 (a weekday). Image from GOOGLE EARTH.

Figure S3. Number of vehicles per hectare in three of the main parking lots (data pooled) in the campus Darcy Ribeiro of the Universidade de Brasília. Data were obtained by satellite images of GOOGLE EARTH for 2015. Boxplot shows median (weekdays: 648, weekends: 53), quartiles, minimum and maximum values. Samples represented by the number of daily images are shown by grey dots (weekends, n = 93) and triangles (weekdays, n = 84).