Urban noise restricts, fragments, and lightens sleep in Australian magpies[☆]

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ABSTRACT

Urban areas are inherently noisy, and this noise can disrupt biological processes as diverse as communication, migration, and reproduction. We investigated how exposure to urban noise affects sleep, a process critical to optimal biological functioning, in Australian magpies (*Cracticus tibicen*). Eight magpies experimentally exposed to noise in captivity for 24-h spent more time awake, and less time in non-rapid eye movement (non-REM) and REM sleep at night than under quiet conditions. Sleep was also fragmented, with more frequent interruptions by wakefulness, shorter sleep episode durations, and less intense non-REM sleep. REM sleep was particularly sensitive to urban noise. Following exposure to noise, magpies recovered lost sleep by engaging in more, and more intense, non-REM sleep. In contrast, REM sleep showed no rebound. This might indicate a long-term cost to REM sleep loss mediated by noise, or contest hypotheses regarding the functional value of this state. Overall, urban noise has extensive, disruptive impacts on sleep composition, architecture, and intensity in magpies. Future work should consider whether noise-induced sleep restriction and fragmentation have long-term consequences.

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1. Introduction

Sleep serves many important and non-mutually exclusive functions. Sleep has been implicated in the maintenance of the brain (Xie et al., 2013; Tononi and Cirelli, 2016; Fultz et al., 2019; Zada et al., 2019), improvements in attention, motivation, memory (Van Dongen et al., 2003; Dieckelmann and Born, 2010; Tononi and Cirelli, 2016) and learning (Huber et al., 2004; Derégnaucourt et al., 2005), brain maturation early in life (Scriba et al., 2013; Kayser et al., 2014), and energy homeostasis (Siegel, 2009; Schmidt et al., 2017). The essential value of sleep is further implied by the apparent absence of any truly sleepless animal (Ungurean et al.,

2020), as well as the evolutionary persistence of sleep under the risk of predation (Lima et al., 2005), and in the face of competing waking demands (Lesku et al., 2012; Aulsebrook et al., 2016; Rattenborg et al., 2016; Ferretti et al., 2019).

The expansion of the urban world has led to a dramatic increase in anthropogenic noise infiltrating natural spaces (Barber et al., 2010). Environmental noise has diverse impacts on wild animals, including decreased breeding success (Schroeder et al., 2012; Potvin et al., 2015; Ernstes et al., 2016), diverted migratory paths (McClure et al., 2013; McClure et al., 2016), altered vocalization frequency and timing (Brumm, 2004; Fuller et al., 2007; Kight and Swaddle, 2015), and elevated stress responses (Wright et al., 2007; Kleist et al., 2018). Although noise associated with urban environments decreases the amount of sleep in humans (Weyde et al., 2017; Basner et al., 2014; Fyhri et al., 2010; Frei et al., 2014) and laboratory rodents (Rabat et al., 2005; Rabat, 2007; Bosquillon de Jenlis et al., 2019), whether such pollution similarly restricts sleep in wildlife, or impairs sleep-related functions, is unknown. Indeed, to our knowledge, no study has investigated how urban noise

impacts sleep physiology in wildlife.

We used behaviour and electrophysiology to investigate how experimental exposure to urban noise affects sleep in a native bird, the Australian magpie (*Cracticus tibicen tyrannica*). Australian magpies are an ideal species to address this question as they are common birds found across much of Australia; they occupy urban, noise-polluted areas, and they tolerate close human interaction (Ashton et al., 2018; Kaplan, 2019). Utilizing miniature electroencephalogram (EEG) dataloggers (Vyssotski et al., 2009), we recorded the electrical activity of the brain to provide insight into the amount, composition, continuity, and intensity of sleep in magpies. Birds and mammals have two kinds of sleep: non-rapid eye movement (non-REM) and REM sleep, each thought to serve a unique, or perhaps complementary, function (Lesku and Rattenborg, 2014; Vyazovskiy and Delogu, 2014). Furthermore, when birds and mammals are kept awake, they recover lost non-REM sleep by sleeping more, and/or more intensely. Non-REM sleep intensity is reflected by increased incidence and/or amplitude of EEG slow waves, or 'slow wave activity' (SWA; Rattenborg et al., 2009; Tobler, 2011). Using these data, we were able to quantify any changes to sleep in wild-caught magpies exposed to urban-recorded, experimentally controlled noise in a laboratory context. We anticipated that exposure to urban noise would disrupt sleep, and that lost sleep would be recovered when the noise was turned off.

2. Methods

(a) Animals and housing conditions

In January 2019, we captured 12 wild adult Australian magpies (equal numbers of each sex) in the City of Melbourne, Australia, using a walk-in trap baited with grated cheese. All magpies had previously inhabited urban parklands and were captured within 6 km of one another. Of these birds, we ultimately obtained complete data from eight individuals; see *Supplementary Information*. Magpies were transported to an indoor facility at nearby La Trobe University where they were housed individually in aviaries (1.8 m high x 1.8 m deep x 0.9 m wide) in one of two sex-mixed rooms with similar configurations (Supplementary Fig. 1). Aviaries were left uncovered, allowing the magpies to both see and communicate with each other. Each aviary contained three perches: two rectangular plank perches (15 cm wide), one 1.3 m and the other 0.45 m above the ground, and a dowel perch 0.45 m above the floor. The birds routinely slept on the highest perch, therefore one video camera with infrared capabilities was positioned at one end of the high rectangular perch, and a second was mounted on the aviary door focussing on the lower perches and the floor of the aviary. Magpies were fed 55 g of a mixture of minced meat and an insectivore mix (Wombaroo Food Products, Australia) once per day (0900 $\pm$ 1 h). Water was provided *ad libitum* via a large bowl, providing the magpies a place to both drink and bathe. Aviary floors were covered in woodchips. To provide enrichment, 15—20 mealworms were scattered daily throughout the woodchips giving the magpies opportunity to forage. Rooms were temperature controlled (22 $\pm$ 5 °C) and insulated from all external light. Room lighting (153 $\pm$ 18 lux) was set to a 12-h light (0700—1900 h), 12-h dark (1900—0700 h) photoperiod. A night light that mimicked the intensity of moonlight (average ~0.1 lux at the level of the sleeping perch) were placed in each room allowing the magpies to move safely during the night.

(b) Recording sleep

To investigate the impact of urban noise on sleep, we implanted magpies with electroencephalogram (EEG) and electromyogram (EMG) electrodes using standard stereotaxic procedures (see *Supplementary Information* for details). All electrode wires were soldered to a small connector (6.0 mm wide) fixed to the top of the head with dental acrylic, forming a 'head plug' to which the EEG/EMG datalogger would later connect. Magpies were given a minimum of two weeks to recover from surgery before the experiment began. To record the EEG and EMG, we captured magpies by hand and connected the datalogger (Neurologger 2 A), powered by two zinc air batteries, to the head plug. The datalogger continuously recorded the EEG and EMG, and included an inbuilt tri-axial accelerometer that measured head acceleration, for 5 days; all signals were sampled at 100 Hz. The datalogger and batteries (together 6 g) were wrapped in kinetic thread seal tape to protect them from moisture and physical damage. Magpies were given a minimum of 24-h after attachment of the datalogger to adjust to its presence before baseline recordings began. Magpies showed no change in behaviour when fitted with the dataloggers.

(c) Experimental design

Effects of recorded urban noise on sleep and recovery — We used a repeated measures design to investigate the impact of urban noise playback on magpie sleep. The playback stimulus consisted of a single track of urban noise (including cars, motorcycles, trams, people, dogs, and wildlife) recorded over a 24-h period, on a weekday, at a busy roadside park in Melbourne, occupied by magpies. The playback was recorded using a Bioacoustic Audio Recorder (BARs, Frontier Labs; sampling rate: 44.1 kH gain, 20 dB); positioned 30 m from the nearest road. All sound levels presented were A-weighted decibels (dBA). This recording was unedited and highly heterogeneous, containing no repeating components, and a large variety of sounds in an unpredictable sequence including traffic, human voices, animal noises, and environmental noise. The recording was played back at amplitudes observed in the wild (Melbourne urban park range: 50—70 dBA, average over 24 h) and therefore represented a realistic urban sound environment. The recording was broadcast to the magpies through an omnidirectional speaker (Ultimate Ears Boom 2) placed in the centre of each room, such that three of the eight magpies were closer (<1 m) to the speaker, and the others were farther away. A sound level logger (Sound Level Meter Data Logger NSRT mk2, type 1, Convergence Instruments), positioned approximately 3.5 m from the speaker, allowed us to monitor noise levels in the room throughout the experiment.

The experiment involved a 3.5-day cycle, starting at lights-off (1900 h) on Day 1. The first 24-h after the lights were turned off on Day 1 served as a baseline during which there was no playback, and noise levels averaged 42 dBA at 3.5 m (Supplementary Fig. 2); a ventilation and air-conditioning system present in each room was the source of the low-level noise, whereas magpie carols and calls were the source of the high-level noise. The magpies were then subjected to 24-h of noise averaging 66 dBA in amplitude at 3.5 m starting at lights-off (night-time: 67 $\pm$ 1.0 dBA; daytime: 65 $\pm$ 1.2 dBA). This sound level was similar to amplitudes measured at other habitats occupied by magpies throughout Melbourne, is well below the safe threshold for humans, and is within the range of noise pollution found in other metropolitan areas (Brown et al., 2015). Noise exposure was followed by 36-h of recovery under conditions identical to the initial baseline (no playback, average 42 $\pm$ 6 dBA).

(d) Analysing sleep

To analyse the effects of urban noise on sleep we utilised the supervised machine-learning algorithm Somnivore™ (Allocca

et al., 2019) to score wakefulness, non-REM sleep, and REM sleep in 4 s epochs. Somnivore makes use of all available channels when scoring signals; scoring was manually checked for systematic errors and artefacts (see *Supplementary Information* for details).

(e) Statistical analysis

We conducted all analyses in the statistical environment R version 3.5.2 (R Development Core Team, 2018). We used linear mixed effects models to investigate effects of urban noise exposure on the amount of each state (wakefulness, non-REM and REM sleep), as well as total number and duration of bouts of wake and non-REM sleep during both the night-time and daytime. In addition, we investigated the percentage of total night-time sleep composed of REM sleep, night-time EEG slow wave activity (SWA) during non-REM sleep, as well as total number and duration of REM sleep bouts during the night. Magpies had little non-REM or REM sleep during the daytime; we therefore chose to exclude non-REM sleep SWA, the percentage of total sleep composed of REM sleep, and the duration and number of REM sleep bouts from daytime analyses. Daytime and night-time data were modelled separately for each experiment, with *day/night*, time of night (*quarter*), and an interaction term between *day/night* and *quarter* as categorical fixed effects. *Bird identity* was included as a random effect in all models to account for repeated measures. *Sex* was initially included as a fixed effect but was removed as it did not significantly impact any sleep variable (range: $0.07 < p < 0.99$). Models were fitted using the package *lme4* (Bates et al., 2015). Dependent variables were transformed [$\log(x+1)$] to meet assumptions for model residuals, assessed by visually inspecting model residuals, with two exceptions. For models of both night and daytime wakefulness, we modelled the log transformation [$\log(x)$]. For models of the percentage of night-time non-REM sleep, variance in model residuals decreased with the mean; we therefore modelled the log transformation of the inverse [$\log(100-\%\text{non-REM sleep})$], then inversed output values for interpretation. We used a type 3 analysis of variance (ANOVA) to test for overall effects of fixed factors or interactions in the models (Tables 1 and 2). We ran *post hoc* paired t-tests to determine at which level significance was reached for the amount, duration (expressed as a 12-h or night/day-time quarterly mean) and number of each state between treatments (12-h) and quarters (3-h).

To determine whether non-REM sleep intensity was influenced by urban noise, we measured SWA. SWA captures the incidence and size of EEG slow waves during non-REM sleep, and is typically quantified as c. 0.5–4 Hz spectral power density during non-REM sleep (Rattenborg et al., 2009; Tobler, 2011). SWA increases and decreases with time awake and asleep, respectively, in other birds and mammals (Rattenborg et al., 2009). Furthermore, SWA predicts non-REM sleep depth in mammals (Neckelmann and Ursin, 1993). For these collective reasons, SWA is thought to reflect sleep need (or pressure) and non-REM sleep intensity (or depth). To calculate SWA, we performed fast Fourier transforms on epochs in 0.39 Hz bins using RemLogic v. 3.4.4 (Embla Systems, Pleasanton, United States) between 0.78 and 3.91 Hz during non-REM sleep, excluding epochs containing artefacts and transitions between states. SWA was calculated for each quarter (3-h) of the day and night, and expressed as a percentage of mean non-REM sleep-related SWA across the entire 12-h baseline night. We used paired t-tests to compare the amount of SWA in each treatment per timepoint. In addition, we used analysis of variance (ANOVA) to look for changes in sleep intensity over time (throughout the night) and compare intensity across days. Unless otherwise noted, the values presented in the results are mean ± SE (standard error).

(f) Ethics and permissions

All methods were approved by the La Trobe University Animal Ethics Committee (AEC, 18034). Birds were captured, and ultimately released, with permission from the Department of Environment, Land, Water and Planning (permit number: 10,008,264) and the Australian Bird and Bat Banding Scheme (ABBBS number 1405). One bird died during surgery due to complications while under isoflurane. After experiments were complete, the remaining birds were released in July 2019; eight of the eleven birds were observed in the wild within one month of release. These birds were not equipped with VHF transmitters and so sightings were serendipitous. Furthermore, three birds were sighted one year after release, indicating no long-lasting effects of captivity or surgery.

Table 1
Effects of urban noise exposure on night-time sleep in magpies. Fitted models are LMMs with bird identity as a random intercept. Night-time (12-h) sleep were modelled separately, with night, quarter of the night, and the interaction between night and quarter as categorical fixed effects. Results presented are omnibus tests performed using a type three analysis of variance. Statistically significant results are highlighted in bold.

		Wake			NREM sleep			REM sleep			REM/Sleep[e]			NREM SWA		
	dfn[a]	dfd[b]	F	p	dfd	dfd	dfd	dfd	F	p	dfd	F	p	dfd	F	p
Percentage																
Treatment[c]	3	102	26.90	**<0.01**	101	11.38	**<0.01**	101	26.00	**<0.01**	101	12.62	**<0.01**	98	23.74	**<0.01**
Quarter[d]	3	101	57.64	**<0.01**	101	53.78	**<0.01**	101	83.53	**<0.01**	101	62.32	**<0.01**	97	4.25	**<0.01**
Treatment x quarter	9	101	2.36	**0.02**	101	9.67	**<0.01**	101	1.32	0.23	101	2.40	**<0.01**	97	2.83	**<0.01**
Bout Duration																
Treatment	3	102	3.96	**0.01**	101	23.09	**<0.01**	100	14.05	**<0.01**						
Quarter	3	101	42.92	**<0.01**	101	72.63	**<0.01**	100	5.70	**<0.01**						
Treatment x quarter	9	101	1.47	0.17	101	22.39	**<0.01**	100	0.61	0.79						
Number of Bouts																
Treatment	3	102	59.10	**<0.01**	102	13.04	**<0.01**	100	14.71	**<0.01**						
Quarter	3	101	12.60	**<0.01**	101	101.03	**<0.01**	100	69.82	**<0.01**						
Treatment x quarter	9	101	2.05	**0.04**	101	12.85	**<0.01**	100	0.92	0.51						

Fitted models are LMMs with bird identity as a random intercept. Night-time (12-h) sleep were modelled separately, with night, quarter of the night, and the interaction between night and quarter as categorical fixed effects. Results presented are omnibus tests performed using a type three analysis of variance. Statistically significant results are highlighted in bold.

[a] dfn is degrees of freedom numerator.
[b] dfd is degrees of freedom denominator. Degrees of freedom were calculating using the Satterthwaite method and can vary depending on the response variable.
[c] Treatment is baseline (no noise), treatment (noise exposure), recovery 1 (no noise), and recovery 2 (no noise).
[d] Quarter of night represents a 3-h period of the night.
[e] Percentage of total sleep that is spent in REM sleep.

Table 2

Effects of urban noise exposure on daytime sleep in magpies. Fitted models are LMMs with bird identity as a random intercept. Daytime (12-h) sleep were modelled separately, with day, quarter of the day, and the interaction between day and quarter as categorical fixed effects. Results presented are omnibus tests performed using a type three analysis of variance. Statistically significant results are highlighted in bold.

		Wake			NREM sleep			REM sleep		
	dfn^a	dfd^b	F	p	dfd	F	p	dfd	F	p
Percentage										
Treatment[c]	2	74	0.01	0.99	73	2.78	0.07	73	2.37	0.10
Quarter[d]	3	73	5.52	**<0.01**	73	17.17	**<0.01**	73	4.50	**<0.01**
Treatment x quarter	6	73	0.93	0.48	73	3.25	**<0.01**	73	0.85	0.54
Bout Duration										
Treatment	2	70	3.30	0.04	70	2.35	0.10			
Quarter	3	70	15.17	**<0.01**	70	6.66	**<0.01**			
Treatment x quarter	6	70	3.27	**<0.01**	70	1.54	0.18			
Number of Bouts										
Treatment	2	70	4.49	0.01	70	4.49	0.01			
Quarter	3	70	15.75	**<0.01**	70	17.17	**<0.01**			
Treatment x quarter	6	70	2.64	0.02	70	2.82	0.02			

Fitted models are LMMs with bird identity as a random intercept. Daytime (12-h) sleep were modelled separately, with day, quarter of the day, and the interaction between day and quarter as categorical fixed effects. Results presented are omnibus tests performed using a type three analysis of variance. Statistically significant results are highlighted in bold.

[a] dfn is degrees of freedom numerator.
[b] dfd is degrees of freedom denominator. Degrees of freedom were calculating using the Satterthwaite method and can vary depending on the response variable.
[c] Treatment is baseline (no noise), treatment (noise exposure), and recovery 1 (no noise).
[d] Quarter of night represents a 3-h period of the day.

3. Results

(I) Magpie sleep composition

Baseline − Magpies are strongly diurnal (Fig. 1). Magpies slept 10.8 h over the 24-h baseline day, and little of this (5.4 ± 1.0%) occurred during the daytime. Conversely, non-REM and REM sleep comprised 72.7 ± 1.2% and 12.2 ± 1.0% of the night, respectively, with the remaining 15.1 ± 2.0% occupied by wakefulness. The percentage of total sleep time allocated to REM sleep was 14.4 ± 1.2% (Table 3). The amount of non-REM sleep declined across the night ($F_{11,84} = 14.41$, p < 0.01), arising from progressively shorter non-REM sleep bouts ($F_{11,84} = 5.02$, p < 0.01), despite there being more episodes overall ($F_{11,84} = 23.48$, p < 0.01). As the night progressed, the amount of REM sleep increased ($F_{11,84} = 17.51$, p < 0.01), brought about by more and longer REM sleep bouts (number: $F_{11,81} = 19.87$, p < 0.01; duration: $F_{11,81} = 4.15$, p < 0.01). One hour before lights-on, the magpies began to wake up for the day, and the large amount of night-time sleep was replaced by large amounts of daytime wakefulness. The low amounts of daytime sleep consisted primarily of non-REM sleep during a mid-day siesta (1000−1300 h). Magpie SWA during non-REM sleep declined significantly across the baseline night ($F_{3,28} = 2.95$, p = 0.05).

To better understand the sleep patterns of magpies, we also quantified total bout number and duration for each state (Table 4). During the night, magpies woke up 273 ± 27 times, and entered non-REM sleep and REM sleep 938 ± 20 and 698 ± 35 times, respectively. The similar number of non-REM and REM sleep episodes, and foreknowledge that birds and mammals only enter REM sleep from non-REM sleep, means that most bouts of non-REM sleep terminated with REM sleep. Mean bout length varied between states: bouts of night-time wakefulness were 28 ± 3 s in duration; non-REM sleep episodes were 34 ± 1 s; and REM sleep bouts were 8 ± 0 s. During the day, the number of wake bouts were similar to the night (282 ± 61), but were considerably longer in duration (201 ± 43 s). There were far fewer (289 ± 60) and shorter (8 ± 1 s) episodes of daytime non-REM sleep, relative to those at night. REM sleep occurred infrequently during the day (total number of REM sleep bouts across all birds: 119, average: 18 ± 8); thus, daytime REM sleep was not analysed further.

(II) Effects of urban noise on sleep and recovery sleep

Night-time sleep during noise playback - Exposure to urban noise affected both the amount and composition of night-time sleep, with impacts observed both across the entire treatment night and in individual quarters of the night (Table 1). When exposed to noise, the time spent awake at night doubled to 32.8 ± 3.7%, non-REM sleep decreased to 61.6 ± 3.2%, and REM sleep was halved to 5.6 ± 1.3% (Table 3, Fig. 2). The percentage of night-time total sleep time allocated to REM sleep also decreased during the noise playback (8.0 ± 1.7%; t = 4.76, p < 0.01). During the first 3-h of exposure to urban noise, bouts of non-REM sleep were significantly shorter, and more numerous, compared to the baseline night; REM sleep episodes were both shorter and fewer during the noise presentation, reflecting sleep fragmentation (Table 4, Fig. 3). There was no statistical difference between the two experimental rooms in terms of the amount of sleep states during the treatment night (wake: t = −0.93, p = 0.40; non-REM sleep: t = 1.29, p = 0.26; REM sleep: t = −0.29, p = 0.78).

Night-time sleep recovery − Exposure to noise had a lasting impact that carried over into the recovery nights (Table 1). During the first recovery night, the amount of wakefulness decreased to 13.2 ± 0.6%, compared to the baseline night (t = 5.62, p < 0.01), indicating that the magpies slept more on the recovery night; however, individually, non-REM sleep (t = −0.92, p = 0.39) and REM sleep were largely unchanged (t = −1.01, p = 0.35; Table 3, Fig. 2). Moreover, there were fewer bouts of wakefulness, but the other architectural features of sleep were unchanged from baseline (Table 4, Fig. 3). On the second recovery night, no state differed from baseline in overall amount (wake: t = 1.19, p = 0.28; non-REM sleep: t = −0.93, p = 0.39; REM sleep: t = −0.05, p = 0.96), but there were again fewer bouts of wakefulness, and now non-REM sleep bouts were also fewer and longer, reflecting sleep consolidation.

Day-time sleep during noise playback − Noise did not have a strong impact on day-time sleep (Table 2). During the day with noise playback (following a night with noise playback), time spent awake (95.0 ± 2.7%; t = −0.18, p = 0.86), in non-REM sleep (4.9 ± 2.7%; t = 0.13, p = 0.90), and in REM sleep (0.6 ± 0.0%; t = 1.57, p = 0.16), were all similar to baseline values (Table 3, Fig. 2).
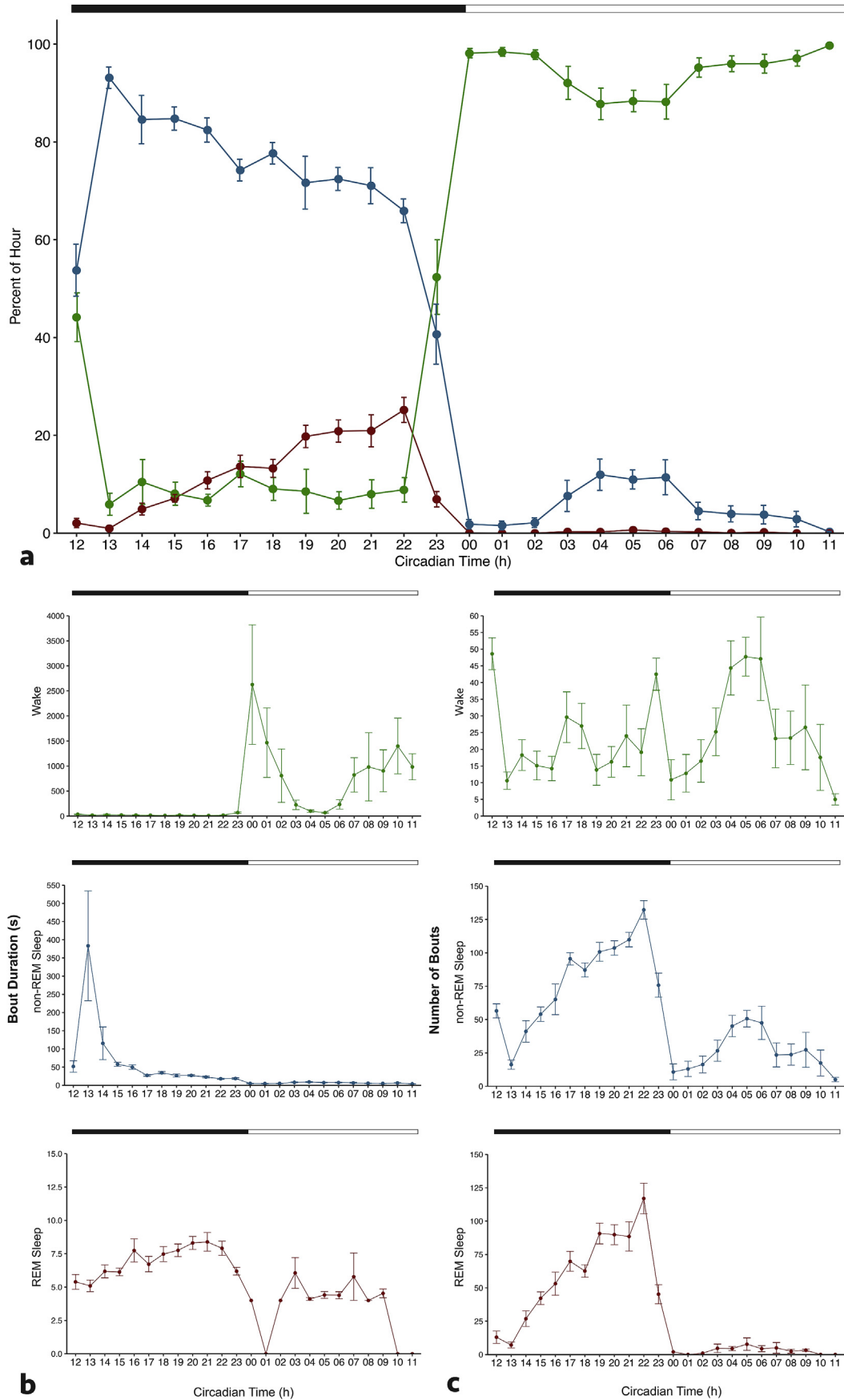
Fig. 1. Magpie sleep architecture under baseline conditions. (a) Timing and amount (%) of wake (green), non-REM sleep (blue), and REM sleep (red) across the 24-h undisturbed recording, and the (b) duration and (c) number of state episodes. Time of day is expressed as circadian time, whereby lights were switched on/off at 00/12 h, respectively. The black horizontal bar along the top of the plot indicates night; the white bar reflects day. All data are shown as mean ± SE.

Table 3
Effects of noise on the percentage of wake, non-REM sleep, and REM sleep, and the percentage of sleep allocated to REM sleep (%REM sleep) in magpies. Magpies were recorded during an undisturbed 24-h day (Baseline), followed by 24-h of noise exposure (Treatment), and ending with two recovery periods (Recovery R1 and R2; 24-h and 12-h respectively). Values are presented as mean ± SE, along with P-values from paired t-tests that compared between nights (top) and days (bottom). The %REM sleep during the day was rare and excluded. Statistically significant results are highlighted in bold.

Night-time Sleep							
	Night 1 Baseline (B)	Night 2 Treatment (T)	Night 3 Recovery (R1)	Night 4 Recovery (R2)	P B − T	P B − R1	P B − R2
Wake	15.1 ± 0.7	32.8 ± 3.7	13.2 ± 0.6	13.7 ± 0.4	t = −4.36 **p < 0.01**	t = 5.62 **p < 0.01**	t = 1.19 p = 0.28
NREM	72.7 ± 1.2	61.6 ± 3.2	73.6 ± 1.6	74.6 ± 1.2	t = 3.28 **p < 0.01**	t = −0.92 p = 0.39	t = −0.93 p = 0.39
REM	12.2 ± 1.0	5.6 ± 1.3	13.1 ± 1.5	11.8 ± 1.1	t = 5.95 **p < 0.01**	t = −1.01 p = 0.35	t = −0.05 p = 0.96
REM/Sleep	14.4 ± 1.2	8.0 ± 1.7	15.1 ± 1.7	13.6 ± 1.3	t = 4.76 **p < 0.01**	t = −0.71 p = 0.50	t = 0.19 p = 0.86
Daytime Sleep							
	Day 1 Baseline (B)	Day 2 Treatment (T)	Day 3 Recovery (R1)		P B - T	P B − R1	
Wake	94.6 ± 1.0	95.0 ± 2.7	94.1 ± 1.3	—	t = −0.18 p = 0.86	t = −0.49 p = 0.64	
NREM	5.2 ± 1.0	4.9 ± 2.7	5.8 ± 1.2	—	t = 0.13 p = 0.90	t = −0.63 p = 0.55	
REM	0.2 ± 0.1	0.6 ± 0.0	0.1 ± 0.1	—	t = 1.57 p = 0.16	t = 1.69 p = 0.14	

Table 4
Effects of noise on the number and duration of bouts of wake, non-REM sleep and REM sleep in magpies. Magpies were recorded during an undisturbed 24-h day (Baseline), followed by 24-h of noise exposure (Treatment), ending with two recovery periods (Recovery R1 and R2; 24-h and 12-h respectively). Values are presented as mean ± SE, along with P-values from paired t-tests that compared between nights (top) and days (bottom). Daytime REM sleep was rare and excluded from analysis. Statistically significant results are highlighted in bold.

Night-time Sleep								
		Night 1 Baseline (B)	Night 2 Treatment (T)	Night 3 Recovery (R1)	Night 4 Recovery (R2)	P B - T	P B - R1	P B − R2
Wake	no. bouts	273.4 ± 27.0	780.4 ± 91.9	222.0 ± 29.8	219.0 ± 17.2	t = −5.61 **p < 0.01**	t = 2.67 **p = 0.03**	t = 3.03 **p = 0.02**
	bout length (s)	28.1 ± 2.8	20.8 ± 2.6	43.9 ± 12.3	44.3 ± 12.5	t = 3.05 **p = 0.02**	t = −1.32 p = 0.23	t = −1.67 p = 0.15
NREM	no. bouts	937.9 ± 20.3	1101.9 ± 68.1	925.3 ± 38.4	861.9 ± 35.6	t = −2.81 **p = 0.03**	t = 0.58 p = 0.58	t = 2.43 **p = 0.05**
	bout length (s)	33.7 ± 1.2	25.1 ± 2.4	35.0 ± 2.2	37.9 ± 2.1	t = 3.8 **p < 0.01**	t = −1.06 p = 0.33	t = −2.40 **p = 0.05**
REM	no. bouts	698.1 ± 34.9	381.4 ± 67.5	732.0 ± 47.0	668.7 ± 37.9	t = 5.80 **p < 0.01**	t = −1.07 p = 0.32	t = 0.41 p = 0.70
	bout length (s)	7.5 ± 0.3	6.0 ± 0.5	7.6 ± 0.5	7.5 ± 0.5	t = 3.03 **p = 0.02**	t = −0.36 p = 0.73	t = −0.61 p = 0.56
Daytime Sleep		Day 1 Baseline (B)	Day 2 Treatment (T)	Day 3 Recovery (R1)		P B - T	P B − R1	
Wake	no. bouts	282.3 ± 60.5	219.0 ± 84.8	278.4 ± 73.8	—	t = 1.05 p = 0.33	t = 0.55 p = 0.60	
	bout length (s)	200.5 ± 42.6	1170.6 ± 740.0	250.5 ± 96.3	—	t = −1.35 p = 0.22	t = −1.00 p = 0.36	
NREM	no. bouts	288.5 ± 59.8	220.3 ± 84.7	282.3 ± 73.8	—	t = 1.11 p = 0.30	t = 0.63 p = 0.55	
	bout length (s)	8.1 ± 0.6	8.0 ± 1.2	12.0 ± 3.2	—	t = 0.17 p = 0.87	t = −1.25 p = 0.26	

During day-time exposure, duration and number of bouts of wakefulness were longer, but non-REM sleep, and REM sleep were all similar to baseline values (Table 4).

Daytime sleep recovery − During the recovery day, the amount, duration, and number of bouts of wakefulness, non-REM sleep, and REM sleep were all similar to baseline values (Table 2, Table 3, Table 4).

Slow wave activity at night − Noise had a strong effect on non-REM sleep SWA, showing impact to the entire treatment night and individual quarters throughout the night (Table 1). SWA during exposure to urban noise was lower relative to baseline

$(F_{1,62} = 29.52, p < 0.01)$ and did not vary across the night $(F_{3,28} = 1.95, p = 0.14;$ Fig. 4). Over the first recovery night, SWA progressively declined $(F_{3,28} = 4.86, p < 0.01)$, and was higher relative to baseline, reflecting non-REM sleep homeostasis. SWA during the second recovery night was not different from baseline values $(F_{1,54} = 0.51, p = 0.48)$.

Slow wave activity during the day − There was less than 1 h of non-REM sleep across each of the 12-h days. Owing to the paucity of daytime non-REM sleep-related SWA data, we did not include it in our analysis.

4. Discussion

We found that Australian magpies experimentally exposed to recorded urban noise in captivity had restricted, fragmented, and lighter sleep compared to baseline conditions. We provide evidence that lost non-REM sleep was recovered by sleeping more, and more intensely, the following night, when the playback was absent. We found no evidence for the recovery of lost REM sleep, which might serve to challenge the idea for an essential restorative function of this state. Overall, these findings provide, to our knowledge, the first experimental evidence that urban noise disrupts sleep in wildlife.

How does urban noise exposure affect magpie sleep? Magpies exposed to noise at night spent more time awake, less time in non-REM and REM sleep, and allocated less time asleep to REM sleep than they did during a quiet night. Sleep during noise exposure was more fragmented, with magpies waking up more often and sleeping for shorter durations. When (non-REM) sleep did occur, it was less intense. Noise had no clear effects on sleep during the day, perhaps because magpies typically spent so much of the day awake under undisturbed conditions.

Magpies exposed to urban noise recovered at least some lost non-REM sleep on the subsequent (quiet) 24-h day. This was shown by the increase in the time spent in non-REM sleep during the first part of the recovery night, and by the increase in non-REM sleep intensity during the recovery night. These findings are consistent with studies on other birds and mammals showing that these animals compensate for reductions in sleep primarily by increasing subsequent non-REM sleep intensity (Jones et al., 2008; Martinez-Gonzalez et al., 2008; Lesku et al., 2011a, 2012; Rattenborg et al., 2016; van Hasselt et al., 2019). Magpies did not experience a rebound in REM sleep, which is consistent with a previous study (Aulsebrook et al., 2020). During noise exposure, magpies lost (on average) 47 min of REM sleep over the 12-h night, and throughout the two recovery nights, only gained back four of the lost minutes. This result was unexpected, as other birds have more REM sleep following extended periods of wakefulness (Jones et al., 2008; Martinez-Gonzalez et al., 2008; Rattenborg et al., 2009; Lesku et al., 2011a, Tisdale et al., 2018). However, other animals either have little REM sleep (Gravett et al., 2017; Davimes et al., 2018) or, like magpies, (apparently) lack REM homeostasis (Lyamin et al., 2008, 2018). Indeed, a recent study on starlings (*Sturnus vulgaris*) found no evidence for REM sleep homeostasis, despite two independent durations of sleep loss (van Hasselt et al., 2019). Further experimental work is needed to better understand sleep regulation in magpies. Nonetheless, similar to work on humans, our findings reveal that avian sleep is also disrupted by urban noise (Rabat et al., 2007; Fyhri et al., 2010; Elmenhorst et al., 2012).

There are a variety of non-mutually exclusive mechanisms by which noise might have affected sleep in our study. First, particular sounds in the recorded noise may have triggered a behavioural response independent of sound amplitude *per se*. Our noise treatment was a recording of urban noise and therefore included noises with varying amplitudes and frequencies, such as dogs barking, humans talking, other wildlife, and diverse noises common in an urban environment. Certain sounds could have triggered anti-predator and vigilance behaviours during the night (Meillère et al., 2015; Yorzinski et al., 2015; McBlain et al., 2020) and therefore caused sleep disruptions. Second, the noise itself may have been novel and only played over a single, 24-h period. Magpies had lived in quiet rooms (42 dBA) for over two months prior to the experiment and were therefore adjusted to a non-urban sound environment. We tried to minimize any novelty effect of the noise, by exposing the birds to the 24-h noise recording (25 days) before the experiment began. Furthermore, two of the birds had to
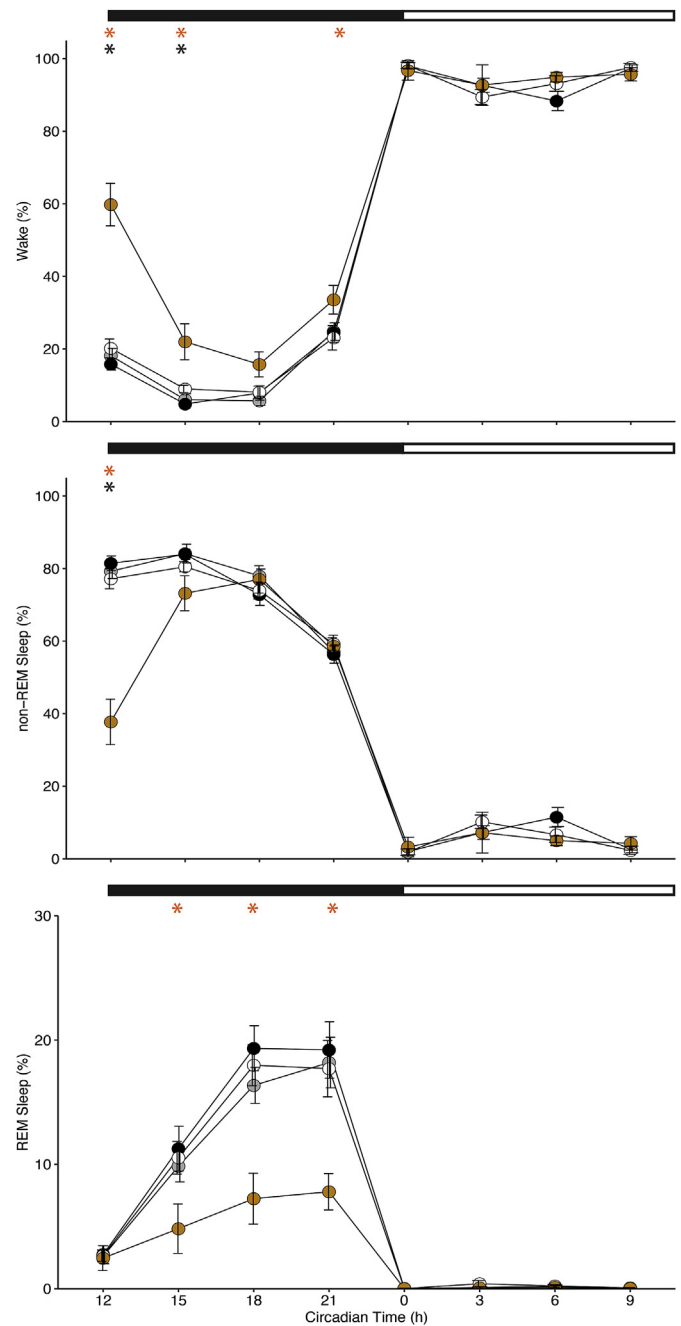

Fig. 2. Effects of urban noise on the percentage of wake, non-REM and REM sleep. Data are summarised as quarterly (3-h) time bins for the baseline (open), noise treatment (orange; lasted the entire 24-h day), first (black) and second (grey) recovery days. Time of day is expressed as circadian time, whereby lights were switched on/off at 0/12 h, respectively. The black horizontal bar along the top of the plot indicates night; the white bar reflects day. All data are shown as mean ± SE; asterisks denote a significant difference between the quarter of that colour-coded day compared to baseline. For example, there was significantly more wakefulness during the first, second, and fourth quarter of the noise treatment night relative to baseline.

undergo the experiment twice, and the patterns observed in these birds was similar to the patterns observed overall. For these reasons, it is unlikely that novelty could explain our results. Nonetheless, exposing birds to noise over a longer period of time may help disentangle the effects of novelty versus noise *per se*. Third, the

noise treatment began at lights-off, when the circadian clock favours sleep, and this may have elicited a stress response in the magpies. It is known that noise can cause stress in wildlife (Wright et al., 2007; Kliest et al., 2018), and stressful situations reduce REM sleep disproportionately in pigeons (Tisdale et al., 2018) and rodents (Lesku et al., 2008). It is possible that some sleep disturbance may have been caused by stress at the start of the playback at lights off; however, that acute effect would not explain the chronic disturbance across the entire night. Finally, our experimental birds were not acoustically isolated from one another. The reactions of a few birds could have caused the rest of the birds to react to noise. Magpies are social animals: over the course of two months, the birds in each room had begun to socially interact (i.e. carol/sing together). In the wild, we have observed a single alarm call from

one group triggering a response from several adjacent groups. The reaction of a few magpies could have disturbed the rest of the group; however, testing magpies in the absence of conspecifics would probably have increased stress in this social species (Ashton et al., 2018).

While this study demonstrates that noise exposure can disrupt sleep, it was conducted in captivity and may not reflect magpie responses in the wild (Aulsebrook et al., 2016). The amount of sleep can differ between captive and wild animals (Rattenborg et al., 2008) and our findings will need to be validated in a natural setting. Nevertheless, these results demonstrate that exposure to urban noise can have adverse and diverse effects on sleep, which can carry over into the night following urban noise. Noise-induced reductions of sleep could potentially have detrimental long-term
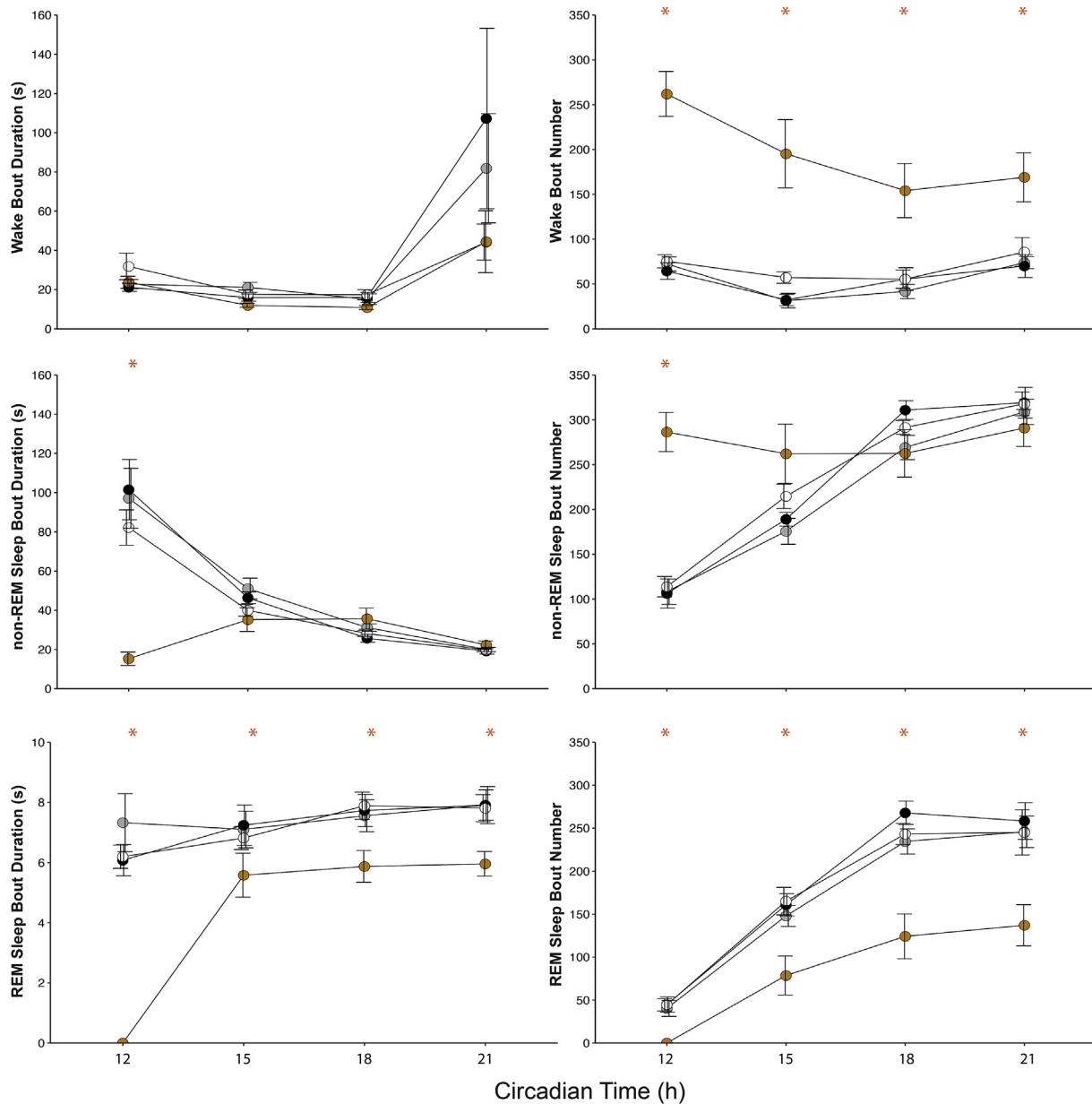

Fig. 3. Effects of urban noise on the bout duration and number of state episodes of night-time wake, non-REM and REM sleep. Data are summarised as quarterly (3-h) time bins for the baseline (open), noise treatment (orange), first (black) and second (grey) recovery nights. Time of day is expressed as circadian time. All data are shown as mean ± SE; asterisks denote a significant difference between the quarter of that colour-coded day compared to baseline. For example, across the entire noise treatment night, bouts of REM sleep were shorter, and less frequent, relative to baseline.
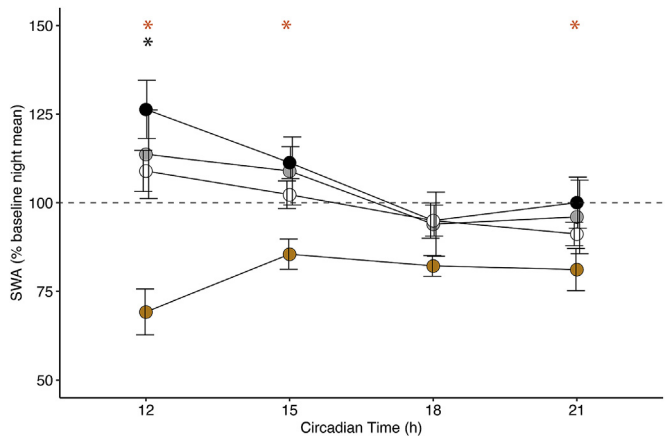
Fig. 4. Effects of urban noise on night-time non-REM sleep-related slow wave activity (SWA; 0.78–3.91 Hz power density). Data are summarised as quarterly (3-h) time bins for the baseline (open), noise treatment (orange; lasted the entire 12-h night), first (black) and second (grey) recovery nights. SWA is expressed as a percentage of the baseline night non-REM sleep mean (i.e. the 100% dashed line). Circadian time plots lights off at 12-h. All data are shown as mean ± SE; asterisks denote a significant difference between the quarter of that colour-coded day compared to baseline. For instance, SWA was significantly lower during most quarters of the noise treatment night, and significantly higher during the first quarter of the first recovery night, relative to baseline.

consequences for health, survival, and reproductive success given sleep's role in energy homeostasis (Schmidt et al., 2017), immune system maintenance (Imeri and Opp, 2009; Irwin, 2015), learning and memory (Derégnaucourt et al., 2005; Kayser et al., 2014), and brain development in early life (Blumberg, 2015), among other functions. Unlike humans, free-living territorial animals have limited options for avoiding or reducing exposure to noise. For this reason, it is important that levels of urban noise are mitigated (e.g. widespread use of electric vehicles would eliminate most traffic noise) in order to protect wildlife from its potential harm.

Our findings suggest many avenues of future research. First, our study only investigated the impact of 24-h of noise. A longer-term study looking at noise exposure over several weeks, or even greater durations, could provide insight into whether animals habituate to the disruptive effects of noise. Second, birds in our study were all from urban environments and may have been accustomed to urban noises (Linley et al., 2018). If true, then the reactions from these birds may have been conservative in comparison to more 'rural' birds. A study comparing birds from rural and urban areas may aid in determining if noise has a greater effect on wildlife from less noise polluted areas. Finally, the control for our experiment was a quiet environment, containing only the sound of an air conditioning unit. In nature, complete noiselessness is rare, and therefore our control may not have been ecologically relevant. An experiment utilizing a control noise recorded from a quieter natural area may provide a better comparison to urban noise.

How do Australian magpies sleep? In the absence of urban noise, magpie sleep followed patterns similar to those observed in other birds (Roth et al., 2006). Across undisturbed nights (i) amounts of non-REM sleep decreased, (ii) amounts of REM sleep increased, (iii) and SWA during non-REM sleep declined (Martinez-Gonzalez et al., 2008; Lesku et al., 2011a; Tisdale et al., 2018). The finer, architectural patterns of magpie sleep were also similar to other birds: non-REM sleep bouts became shorter, and REM sleep bouts became longer and more numerous as the night progressed (Martinez-Gonzalez et al., 2008). Similar to other passerine species (e.g. jackdaw *Corvus monedula*, Szymczak, 1986; rook *Corvus frugilegus*,

Szymczak, 1987; European blackbird *Turdus merula*, Szymczak, 1993), magpies spent very little time asleep during the day; virtually all daytime sleep was non-REM sleep and was clustered in the middle of the day. On average, the amount of REM sleep in magpies was similar to that observed in other songbirds (Roth et al., 2006), as was the (short) duration of REM sleep bouts (van Twyver and Allison, 1972; Rattenborg et al., 2004; Ayala-Guerrero et al., 2003; Lesku et al., 2011b).

In addition to describing the sleep patterns of Australian magpies, we provide the first evidence that even relatively short periods of exposure to urban noise can restrict, fragment, and lighten sleep in wildlife. Our results also question the importance of REM sleep and the functional significance of this sleep state. Noise is pervasive and is increasing in natural spaces globally. Our findings highlight the potential for detrimental consequences for wildlife and the urgent need for further work to establish noise management solutions in urban environments.

Credit author statement

Farley Connelly: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing - original draft, Writing-Reviewing and editing, Funding acquisition; Robin Johnsson: Investigation, Writing-Reviewing and editing; Anne Aulsebrook: Formal analysis, Writing-Reviewing and editing. Raoul Mulder: Conceptualization, Methodology, Writing-Reviewing and editing, Supervision; Michelle Hall: Conceptualization, Methodology, Writing-Reviewing and editing, Supervision; Alexei Vyssotski: Software, Resources, Writing-Reviewing and editing; John Lesku: Conceptualization, Methodology, Writing-Reviewing and editing, Supervision, Funding acquisition

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2020.115484.

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