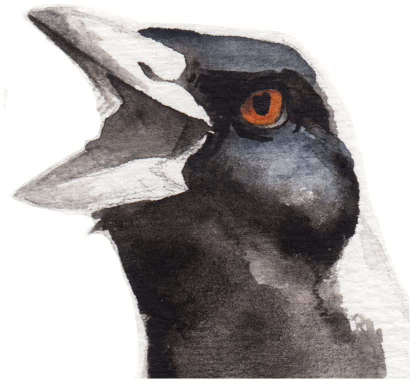

Impacts of anthropogenic pollution on cognition and sleep in an urban bird

Farley Connelly

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"The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka!' but 'That's funny.'"

— Frans de Waal

Abstract

The world is rapidly urbanizing, transforming Earth's natural habitats. While the loss of these habitats is the most visible impact of urban expansion, human population growth has also brought associated phenomena that have the capacity to negatively impact non-human animals. Two key anthropogenic phenomena associated with urban environments have become almost inescapable: anthropogenic noise and artificial light at night. Anthropogenic noise can now be heard in some of the most remote protected areas in the world, while, in the US alone, half of all land mass is exposed to unnatural levels of light at night. There is growing evidence that these environmental 'pollutants' have negative impacts on the behaviours and fitness of urban wildlife. In this thesis, I focus on the potential of these anthropogenic pollutants to disrupt cognitive processes and sleep in an urban-adapted species, the Australian magpie (*Cracticus tibicen).* Wild magpies occupying territories across suburban Melbourne that were exposed to varying levels of urban noise performed similarly on cognitive tasks. Variation in cognitive performance was best explained by age rather than the amplitude of noise to which birds were exposed on a daily basis. I found some evidence that higher sound levels may impair cognitive development, but the effect was observed in only one of four cognitive tasks presented. In captivity, the performance of magpies on similar cognitive tasks was compared under two conditions (experimental exposure to realistic traffic noise, compared to a quiet control). I again found no difference in cognitive performance in the presence or absence of noise. They did, however, perform better on tasks the second time they experienced them, regardless of noise.

Finally, I explored the effect of urban noise and two different colours (blue-rich and blue-reduced) of artificial light at night on sleep in magpies. Magpies exposed to a 24-hour recording of urban noise spent more time awake and less time in non-rapid eye movement (non-REM) and REM sleep throughout the night. Likewise, magpies exposed to artificial light at night spent less time asleep, and their sleep was more fragmented. In addition, blue-rich lighting had a greater effect on sleep than did blue-reduced lighting. My findings shed light on some of the putative pathways by which anthropogenic noise and artificial light can affect key biological processes in suburban wildlife, but also illustrate that not all processes are necessarily detrimentally affected.

Declaration

This is to certify that:

1. This thesis comprises only my original work towards my PhD, except where otherwise stated in the Preface

2. Due acknowledgement has been made in the text to all other material used

3. This thesis contains fewer than 80,000 words, excluding references, tables, figures, and appendices

C. Farley Connelly

9 September 2020

Preface

This thesis contains two chapters that are published in *Environmental Pollution* (*Chapter 4*) and in *Current Biology* (*Chapter 5*). The two other chapters (*Chapter 2* and *3*) are in preparation for publication. There is some necessary repetition between chapters, but I have done my best to keep it to a minimum.

I am the primary author and was the principal contributor to all of the work described in the chapters in this dissertation. My supervisors – Raoul Mulder, John Lesku, and Michelle Hall – provided guidance and advice throughout. All other contributions are recognized in the acknowledgements.

Study design for *Chapters 2* and *3* were created together with my supervisors. I performed the data collection, analysis and writing of these chapters with input from my supervisors. I assisted John Lesku to surgically implant Australian magpies with electrodes, additional help was provided by those listed in the acknowledgments.

Chapter 4 was written with guidance and support of my supervisors and is published in *Environmental Pollution* as: Connelly F, Johnsson R.D., Aulsebrook A.E., Mulder R.A., Hall M.L., Vyssotski A.L., and Lesku J.A. 2020. Urban noise restricts, fragments, and lightens sleep in Australian magpies. Environmental Pollution, 267, 115484.

Chapter 5 was written with guidance and support of my supervisors, Dr. Theresa Jones, and Dr. Anne Aulsebrook. A modified version of this chapter is published in *Current Biology* as (*co-first author): Aulsebrook, A.E.*, Connelly, F.*, Johnsson R.D, Jones T.M., Mulder R.A., Hall M.L., Vyssotski A.L., and Lesku J.A. 2020. White and amber light at night disrupt sleep physiology in birds. Current Biology, 1-7.

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I would not have finished this PhD without the help of two people, Robin Johnson and Annie Aulsebrook. Robin, I will never be able to thank you enough for all your help throughout the last two years of my PhD. I would not have survived six months in those aviaries without you. Annie, thank you for always picking up the phone and providing an answer to all my questions, even when they didn't make sense.

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To the Mulder and Lesku labs, thank you all for being such amazing friends and making a guy from Chicago feel at home in Melbourne.

Thank you to all my family and friends, who supported me along the way. To Mom, thank you for not so subtly saying I could never quit and always providing me the push I needed to keep going. To Dad, thank you for cultivating my love of birds and turning a silly hobby into my favourite competition.

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Table of Contents

ABSTRACT .... **III**
DECLARATION .... **V**
PREFACE .... **VI**
ACKNOWLEDGMENTS .... **VIII**
TABLE OF CONTENTS .... **X**
LIST OF TABLES .... **XII**
LIST OF FIGURES .... **XIII**
CHAPTER 1 – GENERAL INTRODUCTION **1**
1.1 | Impacts of anthropogenic 'pollutants' on urban wildlife 2
1.2 | Urbanisation, anthropogenic noise, and cognitive performance 9
1.3 | Anthropogenic pollutants, cognition, and sleep 12
1.4 | Study Species 15
1.5 | Thesis Outline 16
CHAPTER 2 – DOES ANTHROPOGENIC NOISE AFFECT COGNITIVE PERFORMANCE IN WILD AUSTRALIAN MAGPIES (*CRACTICUS TIBICEN*)? **20**
2.1 | Abstract 23
2.2 | Introduction 23
2.3 | Methods 26
2.4 | Results 37
2.5 | Discussion 42
CHAPTER 3 – COGNITIVE PERFORMANCE IN CAPTIVE AUSTRALIAN MAGPIES IS UNAFFECTED BY URBAN NOISE EXPOSURE. **50**
3.1 | Abstract 51
3.2 | Introduction 51
3.3 | Methods 54
3.4 | Results 68
3.5 | Discussion 71
CHAPTER 4 – URBAN NOISE RESTRICTS, FRAGMENTS, AND LIGHTENS SLEEP IN AUSTRALIAN MAGPIES **79**
4.1 | Abstract 80
4.2 | Introduction 80
4.3 | Methods 82
4.4 | Results 90
4.5 | Discussion 99
CHAPTER 5 – WAKING UP TO THE IMPACTS OF BLUE-RICH LIGHTS: AUSTRALIAN MAGPIES SLEEP MORE UNDER AMBER LIGHT THAN BLUE **106**
5.1 | Abstract 107
5.2 | Introduction 107
5.3 | Methods 111

5.4 | Results 116
5.5 | Discussion 135

CHAPTER 6 – CONCLUSIONS AND FUTURE DIRECTIONS 142

6.1 | General Discussion 143
6.2 | Anthropogenic Noise and Cognition 144
6.3 | Urban Pollution and Sleep 147
6.4 | Concluding Remarks 151

REFERENCES 154

APPENDIX A: SUPPLEMENTARY MATERIALS FOR *CHAPTER 3* 183

Supplementary Figures 184

APPENDIX B: SUPPLEMENTARY MATERIALS FOR *CHAPTER 4* 187

Supplementary Figures 188

APPENDIX C: SUPPLEMENTARY MATERIALS FOR *CHAPTER 5* 191

Supplementary Figures 192
Supplementary Tables 193

List of Tables

Table 2.1. Effect of sound level on cognitive performance on the test battery ...**40**

Table 2.2. Analysis of the proportional differences in performance on the cognitive test battery by magpies at 160 and 290 days post fledging...................**41**

Table 3.1. Effect of noise exposure on cognitive performance **70**

Table 4.1. Effects of noise on the mean wakefulness, non-REM sleep, and REM sleep in magpies ....ERROR! BOOKMARK NOT DEFINED.

Table 4.2. Effects of noise on the mean number and length of bouts of wakefulness, non-REM sleep, and REM sleep in magpies ERROR! BOOKMARK NOT DEFINED.

Table 5.1. Effects of white light on the mean night-time wakefulness, non-REM sleep, and REM sleep in magpies...**120**

Table 5.2. Effects of white light on the mean number and length of bouts of wakefulness, non-REM sleep, and REM sleep in magpies at night....................**121**

Table 5.3. Effects of white light on the mean number and length of bouts of wakefulness and non-REM sleep in magpies during the day **123**

Table 5.4. Effects of amber light on the mean night-time wakefulness, non-REM sleep, and REM sleep in magpies.......ERROR! BOOKMARK NOT DEFINED.**117**

Table 5.5. Effects of amber light on the mean number and length of bouts of wakefulness, non-REM sleep, and REM sleep in magpies at night....................**129**

Table 5.6. Effects of amber light on the mean number and length of bouts of wakefulness and non-REM sleep in magpies during the day **131**

Table 5.7. Effects of light treatment order on the mean wakefulness, non-REM sleep, and REM sleep in magpies..**135**

Table C1. White and amber lux readings...**193**

List of Figures

Figure 1.1. Summary of hypothesised pathways 9

Figure 1.2. Timeline of captive studies 20

Figure 2.1. Anthropogenic noise map of Greater Melbourne, Australia 29

Figure 2.2. Cognitive test battery 36

Figure 2.3. Effect of sound level on cognitive performance on the test battery..39

Figure 2.4. Proportional difference in performance on test battery between ages 160 and 290 days across a noise gradient..42

Figure 3.1. Experimental design and testing regime for (a) control and (b) noise treatment...57

Figure 3.2. Training, associative learning, reversal learning, and spatial memory test boards...63

Figure 3.3. Inhibitory test boards 65

Figure 3.4. Effect of noise treatment on cognitive performance...........................71

Figure 4.1. Magpie sleep architecture under baseline conditions.........................92

Figure 4.2. Effects of anthropogenic noise on the percentage of wakefulness, non-REM, and REM sleep 95

Figure 4.3. Effects of anthropogenic noise on non-REM sleep-related slow wave activity...98

Figure 5.1. Light exposure light regime..112

Figure 5.2. Effects of 4-h of white and amber light exposure on the percentage of wakefulness, non-REM and REM sleep 119

Figure 5.3. Effects of 4-h of white and amber light exposure on non-REM sleep-related slow wave activity 125

Figure 6.1: Summary of hypothesised pathways 144

Figure A1. Room setup to investigate the effect of noise on cognition.............184

Figure A2. Average treatment sound levels of the entire seven-day playback 185

Figure A3. Sonogram of 12-h segment (0100 – 1300) of the noise playback......186

Figure B1. Room setup to investigate the effect of noise exposure on sleep.....188

Figure B2. Sound levels (dBA) during the 24-h control and urban noise playback days 189

Figure B3. Eighty-four-second example of eeg signals in australian magpies .190

Figure C1. Room setup to investigate the effect of light at night on sleep 192

Figure C2. Spectral output of white lighting and amber lighting.......................192

Chapter 1 – General Introduction

Photograph: Australian magpie (*Cracticus tibicen tyrannica*) male and female.

1.1 | Impacts of anthropogenic 'pollutants' on urban wildlife

Human population growth has dramatically altered our natural landscapes through the process of urbanisation and the creation of transportation networks (Swaddle et al., 2015). The expansion of cities has led to habitat degradation, fragmentation, and has caused changes in biodiversity, including species abundance (Benítez-López et al., 2010; Sih et al., 2011). Two of the most pervasive pollutants associated with urbanization are anthropogenic noise and artificial light at night, and the in past two decades research has begun to focus on the effect these pollutants have on wildlife. Below, I summarise the state of research investigating potential impacts on animals, with a focus on birds.

Anthropogenic Noise – Anthropogenic noise is a term used to describe human-generated noise, such as noise caused by vehicles (aircraft, trains, and road vehicles) and industry (power, mining, etc). Noise is deemed "pollution" when it is occurs at an amplitude that is disturbing, unwanted, or interferes with or harms humans or wildlife (Jain et al., 2016). Exposure to anthropogenic noise in the environment is increasingly seen as an important conservation issue (Kunc & Schmidt, 2019). Anthropogenic noise has become an almost omnipresent aspect of the world's soundscape. According to the World Health Organization, traffic-related noise presents a harmful hazard to humans (World Health Organization, 2018) and is associated with cardiovascular disease, cognitive impairment, sleep disruptions, and tinnitus (Barzegar et al., 2015; Elmenhorst et al., 2012; Kabadayi et al., 2018; Smith, 2012; Stansfeld & Clark, 2015; Szalma & Hancock, 2011). These impacts are not isolated to the humans and similar effects are seen in wildlife, both terrestrial and aquatic (Shannon et al., 2016).

The most studied impact of anthropogenic noise is its effect on the vocalisations of birds. Studies have shown that birds alter songs and calls in order to avoid being masked by anthropogenic noise (Nemeth et al., 2013; Potvin, 2017; Slabbekoorn & Peet, 2003). Changes in frequencies in response to traffic noise have been reported in many species including silvereyes (*Zosterops lateralis*) and spotted doves (*Streptopelia chinensis*; Guo et al., 2016; Potvin et al., 2011). Anthropogenic noise also causes birds to adjust the timing of dawn chorus. This was seen in both a single species context in rufous-collared sparrows (*Zonotrichia capensis*; Dorado-Correa et al., 2016) and European robins (*Erithacus rubecula;* Fuller et al., 2007), and within a community of birds, including common blackbirds (*Turdus merula*), song thrushes (*Turdus philomelos*), great tits (*Parus major*), European robins, and common chaffinches (*Fringilla coelebs;* Dominoni et al., 2016). Impacts to the frequency and timing of calls can have severe consequences, and may cause birds to be less attractive or even unrecognizable to conspecifics (Luther et al., 2016).

Noise also has an impact on reproduction and survival of birds. Exposure to noise has been linked to increased nestling mortality and smaller clutch sizes, which has been documented in several species including Western bluebirds (*Sialia Mexicana)* nesting near natural gas plants (Kleist et al., 2018), captive zebra finches exposed to urban noise (Potvin & MacDougall-Shackleton, 2015), house sparrows (*Passer domesticus*) exposed to chronic noise from generators (Schroeder et al., 2012), and great tits breeding in areas of high traffic noise (Halfwerk et al., 2011). Traffic noise also has been shown to both alter an animal's ability to hear and perceive threats (potentially making it more vulnerable to predators ; Meillère et al., 2015); and conversely, to impair its ability to hunt effectively by masking the sound of prey, as is seen in northern saw-whet owls (*Aegolius acadius*; Mason et al., 2016).

Finally, the presence of anthropogenic noise alone can have profound effects on bird distribution and movements. In a pioneering study, the impact of traffic noise on bird diversity in a secluded forest was examined by creating a car-free "phantom road". This road was generated by playbacks of recorded highway noises, played over several days. The effects of this experiment were dramatic, with the road reducing species richness by over 25% (McClure et al., 2013) and altering the age structure of migratory birds, creating an almost impassable barrier for some species (McClure et al., 2017). These studies collectively emphasize the potentially wide-ranging negative effects noise can have on wildlife.

Anthropogenic noise does not only impact birds and humans. A meta-analysis investigating the effects of anthropogenic noise on animals found that noise impacted species of all taxonomic groups studied, including amphibians, arthropods, birds, fish, mammals, and molluscs (Kunc & Schmidt, 2019). Much like birds, the effects are most studied in animals that rely on acoustic cues for communication or predation. In amphibians, frogs exposed to playbacks of airplanes and motorcycles experienced changes to their vocalisations. The effects varied between species: *Rana taipehensis* exhibited both increased call rates and altered the timing of calls; by contrast, *Microhyla butleri, Rana nigrovittata, Kolaoula pulchra,* and *Dendropsophus triangulum* showed decreased call rates (Kaiser & Hammers, 2009*;* Sun & Narins, 2005). In mammals, traffic noise reduced the foraging efficiency of greater mouse-eared bats (*Myotis myotis*) and pallid bats (*Antrozous pallidus*; Bunkley & Barber, 2015; Siemers & Schaub, 2011). In addition, greater mouse-eared bats avoided foraging areas in close proximity to highways and other high amplitude noise sources (Schaub et al., 2008).

Effects are not limited to terrestrial species. Noise pollution impacts aquatic species in a similar way, causing the most disruption to acoustic predators and communication pathways. These effects are most studied in cetaceans, a group renowned for its acoustic capabilities. Noise generated from shipping lanes can have dramatic effects on whales, causing both short- and long-term changes to communication networks (e.g. through song masking) and migratory paths (Dunlop, 2019; Parks et al., 2007). Noise pollution can also cause stress in whales, especially in the family Odontoceti or toothed whales, which has evolved noise-sensitive organs called melons (Erbe et al., 2019). Whales, however, are not unique in this respect; other marine taxa, especially fish, show negative impacts to behaviours, such as foraging (Purser & Radford, 2011), increased stress, and even physiological changes, such as hearing loss or even death due to ocean noise pollution (Weilgart, 2018).

Artificial light at night – Light pollution is the brightening of naturally dark skies by man-made light sources. Much like anthropogenic noise, the amount of artificial light at night is increasing globally with the proliferation of urban environments (Bennie et al., 2015; Kyba et al., 2017). It is estimated that 80% of the world's human population lives under light-polluted skies, and in the United States and Europe that number may be closer to 99% (Falchi et al., 2016). The benefits of artificial light for humans are obvious, but there are also many negative impacts that coincide with artificial light at night, including effects on health, sleep, and cognitive performance (Bedrosian & Nelson, 2017; Navara & Nelson, 2007; Pauley, 2004; Stevens et al., 2007). The increase in artificial light at night is also having unintended impacts on wildlife. Animals have evolved to function around a 24 hour circadian cycle of light and darkness, optimising behaviours around the rising and setting of the sun (Aschoff, 1989; Kronfeld-Schor et al., 2017). Light at night is causing changes to these cycles which can have severe implications for wildlife (Gaston et al., 2014).

In the last 15 years there has been increased interest in the effect light at night may have on urban wildlife (Gaston et al., 2014; Hölker et al., 2010; Longcore & Rich, 2004). Unlike humans, the benefits of artificial lights for wildlife are far less numerous. In the examples that exist, it is often predators who benefit, hunting prey longer into the night (peregrine falcons, *Falco peregrinus,* DeCandido & Allen, 2006) and increasing hunting activity under lights (bats, *Myotis spp.,* Lewanzik & Voigt, 2017). As with anthropogenic noise, one of the more studied impacts of light at night is its effect on vocalisations in birds. Birds exposed to artificial light shifted the timing of their calls, singing earlier in the morning (Dominoni et al., 2013; Kempenaers et al., 2010; Miller, 2006; Nordt & Klenke, 2013). Light at night also caused birds to be more active at night (Alaasam et al., 2018; Ouyang et al., 2017), and some species even prolonged foraging behaviours well after sunset (Russ et al., 2015). Effects of light at night were not limited to behavioural changes and animals exposed to light at night also experienced changes to reproductive success (Kempenaers et al., 2010; Robert et al., 2015), seasonal reproduction (Letallec et al., 2016) and hatchling mortality (Salmon, 2003).

Although there is now a substantial body of research demonstrating that anthropogenic noise and light at night can disrupt a range of biologically important processes in urban animals, relatively little is known about the impact of these pollutants on two key behavioural processes: cognition and sleep. This omission is surprising for several reasons. First, there is growing evidence that light and noise have disruptive effects on cognition in humans (Chellappa et al., 2011; aircraft noise, Clark et al., 2013; Fisk et al., 2018; traffic noise, Lercher et al., 2003). It is therefore plausible and even likely that non-human vertebrates living in urban landscapes could experience similar disruption. Second, cognition is central to the normal functioning of all organisms. In humans, cognitive impairment can have severe consequences including delayed or lost motor coordination (Jafari et al., 2018; Kluger et al., 1997), loss of short and long term memory (Parikh et al., 2016) and overall decline in quality of life (De Vriendt et al., 2012). Cognitive impairment also impacts wildlife, causing complications in imprinting by chicks (McCabe et al., 1992), altering song learning (Peters et al., 2014) and reducing fitness and reproductive success (Huebner et al., 2018; Preiszner et al., 2016). Understanding how cognitive processes are affected by anthropogenic stressors is therefore of critical importance.

Noise and light have the potential to impair the cognitive function of wildlife in two different ways. First, they can cause direct impacts in the form of a distraction or a physiological change. Anthropogenic noise exposure reduces memory and reading comprehension in humans (Clark et al., 2013; Lercher et al., 2003). In birds and rodents, exposure to noise and light is associated with increases in circulating stress hormones (Alaasam et al., 2018; Barzegar et al., 2015; Halperin, 2014; Hu et al., 2014; Ouyang et al., 2017; Raap et al., 2017). Second, they can have an indirect effect through the disruption of sleep (Jafari et al., 2018; Jan Stenvers et al., 2016; Raap et al., 2016; Weyde et al., 2017). In the schematic below I present the framework for my thesis and suggest a possible mechanistic pathway by which urban pollutants effect cognition. Through the remainder of this chapter, I summarise what is known about the elements of this mechanistic pathway.

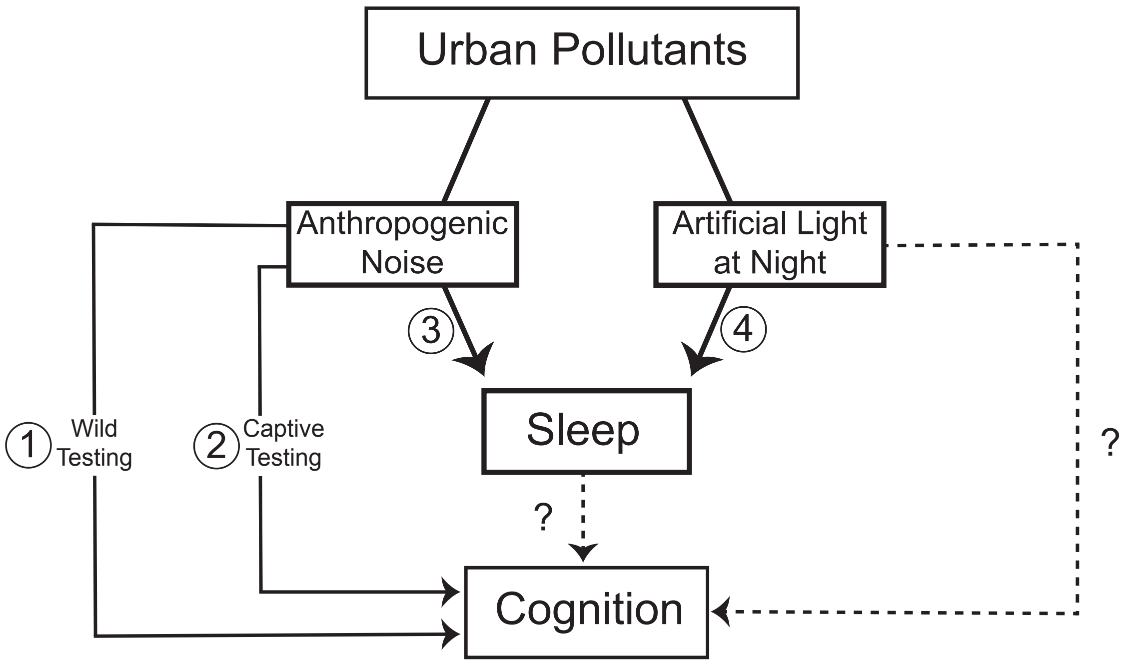

Figure 1.1. Summary of hypothesised pathways (numbered solid lines (1-4) each correspond to a thesis chapter) linking urban pollutants to sleep and cognition which are explored in this thesis. Pathways marked with dotted lines and (?) indicate hypothesised pathways that remain unexplored. Each pathway has several potential mechanisms that could explain the results. These include distraction (Pathways 1, 2), reduction in sleep (Pathways 1, 2), stress (Pathways 1, 2, 3, 4), hormonal changes including melatonin (Pathway 4), and underlying physiological differences (Pathways 1, 2, 3, 4).

1.2 | Urbanisation, anthropogenic noise, and cognitive performance

To date, research on noise exposure and cognition has focused primarily on humans and laboratory rodents. Studies indicate that exposure to urban noise impairs reading comprehension and spatial memory in children through distraction (Clark et al., 2013; Lercher et al., 2003). In adults, it weakens motor coordination and disrupts sleep, causing poorer cognitive performance (Barzegar et al., 2015; Elmenhorst et al., 2012; Kabadayi et al., 2018; Smith, 2012; Stansfeld & Clark, 2015; Szalma & Hancock, 2011) and negatively alters memory in rats and mice (Hu et al., 2014; Jafari et al., 2018; Rabat et al., 2006). It remains unknown whether other urban vertebrates experience similar potential harm.

Effective cognitive functioning is central to many aspects of avian performance. Birds have sophisticated cognitive capabilities, including the ability to complete complex tasks frequently considered to be only within the realm of primates and humans. Birds are able to categorize information and discriminate between objects or images including human faces (American crows, *Corvus brachyrhynchos*, Marzluff et al., 2010; domestic pigeons, *Columba livia domestica,* Stephan et al., 2012), they have a memory capable of storing and recalling the locations of thousands of food items (Clark's nutcracker, *Nucifraga columbiana,* Balda & Kamil, 1992; common ravens, *Corvus corax,* Bugnyar et al., 2007; mountain chickadees, *Poecile gambeli*, Croston et al., 2017; New Zealand robins, *Petroica longipes*, Shaw et al., 2019), they demonstrate theory of mind and are conscious of the presence of potential pilferers when storing food (common ravens, Bugnyar & Heinrich, 2006; Eurasian jays, *Garrulus glandarius,* Shaw & Clayton, 2013, 2014). They are self-aware, recognizing their own reflection (New Caledonian crows, *Corvus moneduloides,* Medina et al., 2011; Eurasian magpie, *Pica pica*, Prior et al., 2016); they are master tool users (New Caledonian crows, Auersperg et al., 2011; rooks, *Corvus frugilegus*, Bird & Emery, 2009) and they understand the notion of displacement (Eurasian jays, New Caledonian crows, and rooks, Jelbert et al., 2014, 2015).

A number of recent studies have investigated the broad effect of urbanization on cognitive function in birds. While there are negative consequences of urban living including pollutants, it has also been suggested that cities might offer a complex new environment that might select for increased behavioural flexibility and improved performance on cognitive tasks (Griffin et al., 2017a, 2017b; Kark et al., 2007). The literature, however, does not broadly confirm this hypothesis. Cognitive testing of birds from rural and urban areas has provided mixed results: for instance, urban and rural Barbados bullfinches (*Loxigilla barbadensis*) showed no difference in performance on learning and reversal tasks (Audet et al., 2016); rural common mynas (*Acridotheres tristis*) outperformed their urban counterparts on learning discrimination tasks (Federspiel et al., 2017), and urban great tits performed better than their rural conspecifics on problem solving tasks (Preiszner et al., 2016). While these studies have demonstrated cognitive differences between birds exposed or not exposed to anthropogenic stressors, they have been unable to directly isolate noise as a causal factor, and to my knowledge, no study has yet explored the impacts of anthropogenic noise on cognitive performance in urban wildlife.

One potential mechanism for noise and light to impact cognition is through distraction. Distraction can impair cognitive performance in two ways. First, external stimuli may impose heavy demands on general attentional resources in order to block unwanted stimulation (much like humans trying to filter out voices while reading at a noisy café). Second, when the distraction is qualitatively similar to the task, competition can occur, limiting an individual's ability to focus on the main task (Craik, 2014). This is often described as cognitive overload and impacts an animal's working memory: its limited cognitive capacity to hold information temporarily (Völter et al., 2019). Noise in particular has the potential to cause both types of distractions. A passing motorcycle or car sounding a horn can cause immediate, unwanted distractions; while higher amplitudes of background noise mask predator noise and warning alarms, forcing individuals to focus harder on potential predators and reduce attention on foraging or mating behaviours. While it was possible to eliminate these distractions in the lab, it is difficult to mitigate these effects in the field and they remain one of the biggest challenges in wild studies of cognition (Janmaat, 2019).

1.3 | Anthropogenic pollutants, cognition, and sleep

From jellyfish (Nath et al., 2017) to platypus (Siegel et al., 1999), sharks (Kelly et al., 2020) to humans, all animals sleep. Sleep is a behaviour closely tied to cognitive processes and one that has the potential to be severely impacted by urbanisation. Sleep is associated with learning, impacting bird song (Derégnaucourt et al., 2005) and performance on learning tasks (Huber et al., 2004). It is essential to the maintenance of attention and behavioural alertness

(Van Dongen et al., 2003), aids in memory consolidation and allows for the formation of new associations (Diekelmann & Born, 2010; Tononi & Cirelli, 2016).

The essential value of sleep is 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 (Aulsebrook et al., 2016; Ferretti et al., 2019; Lesku et al., 2012; Rattenborg et al., 2016). Sleep is defined as a state of reduced responsiveness associated with inactivity that is rapidly reversable, homeostatically regulated, and accompanied by changes in brain activity (Joiner, 2016). Sleep has been implicated in the maintenance of the brain, health and survival (Imeri & Opp, 2009; Irwin, 2015), and improvements in attention, memory and learning (Derégnaucourt et al., 2005; Diekelmann & Born, 2010; Huber et al., 2004; Tononi & Cirelli, 2016; Van Dongen et al., 2003).

In birds and mammals, sleep is composed of two distinct sleep states – rapid eye movement (REM) sleep and non-REM sleep – each believed to serve a unique purpose (Lesku & Rattenborg, 2014; Vyazovskiy & Delogu, 2014). These states are only distinguishable by inspection of a recording of neural activity, visualised by electroencephalogram or EEG. Recording of brain activity requires advanced technology and so historically, sleep was measured by behavioural traits alone. Early recordings of EEG required the connecting of electrodes on the brain via a cable tether to a computer. This process was restrictive and severely limited the species and contexts within which studies could be conducted. In recent years, miniaturisation of technology has revolutionised the measurement of sleep in free-living animals, via lightweight data loggers that can be attached directly to animals (Vyssotski et al., 2009). This allows animals to behave naturally and scientists to record sleep both in both captive and in a more natural, wild context (Lesku et al., 2012; Rattenborg et al., 2008; Vyssotski et al., 2009).

Few studies have investigated the impact of anthropogenic noise and light at night on sleep in wildlife. Humans exposed to noise associated with urban environments show increased sleep disturbances (Basner et al., 2014; Frei et al., 2014; Fyhri & Aasvang, 2010; Weyde et al., 2017) and studies on laboratory rodents exposed to noise mirror these results (De Jenlis et al., 2019; Rabat et al., 2005, 2007). Artificial light at night also impairs sleep in humans and rodents (Erren & Reiter, 2009; Jan Stenvers et al., 2016; Stevens & Zhu, 2015), and it is likely that light at night could disrupt sleep in wildlife (Dominoni et al., 2013; Nordt & Klenke, 2013; Randler, 2014). While these studies suggest that sleep in wildlife could be impacted by noise exposure, to my knowledge no such study exists. In two recently conducted studies (Aulsebrook, 2019), exposure to ecologically relevant urban street lighting disrupted sleep in black swans (*Cygnus atratus*) and pigeons (*Columba livia domestica*), presenting some of the fist evidence that artificial light at night disturbs sleep in wildlife.

There is an additional nuance to the problem of light at night. Cities worldwide are replacing sodium streetlamps with newer light-emitting diodes (LEDs), which are more energy efficient. However, they emit more blue light (from the colour spectrum) which has a particularly strong effect on melatonin. Sleep regulation is partly controlled by the daily rhythms of melatonin, a hormone found in all taxa that is secreted during darkness (Erren & Reiter, 2009; Pandi-Perumal et al., 2006; Zawilska, 1996). If blue-rich lighting does have a stronger effect on melatonin, then the switch to blue-rich LED lighting could severely disrupt sleep in wildlife, as has been found for humans (Pauley, 2004; Van Der Lely et al., 2015). However, a recent study showed that mice slept similarly following exposer to blue-rich and blue-reduced lighting (Mouland et al., 2019), challenging the generality of any effect of blue-rich lighting on sleep. The contrasting results seen in these two species indicate the need for further research investigating how exposure to different colours of light at night may impact sleep in animals.

1.4 | Study Species

The Australian magpie (*Cracticus tibicen*) is a passerine belonging to the family Artamidae. Magpies are abundant in Australia, New Zealand, and New Guinea, occupying variable habitats including city centres and other areas exposed to anthropogenic pollution. I studied the Victorian subspecies (*Cracticus tibicen tyrannica*). This subspecies lives in small family groups, primarily consisting of a dominant male, a dominant female, and sometimes a 'helper' female (Kaplan, 2004). All magpies are dichromatic with females and males exhibiting subtle but distinct variations in their plumage, the male typically having brighter white plumage on the back than females (Kaplan, 2004). Magpies are extremely territorial, spending the majority of their time within a well defended border, endlessly protecting it from neighbouring magpie groups.

Magpies represent an ideal study species for investigating cognitive function. They have highly-developed cognitive capabilities, evidenced by their ability to perform a variety of cognitive tasks (Ashton et al., 2018). In Ashton's study, performance on these tasks was positively correlated with group size. The Western Australia subspecies (*Cracticus tibicen dorsalis)* lives in large family groups containing up to 20 individuals. Individuals are easily distinguishable based on group location, unique physical features or unique numbered leg bands. They can generally be reliably located within a home territory, are typically unconcerned by close human interaction, and willingly habituate to, and participate in cognitive tests (Ashton et al., 2018; Mirville et al., 2016; Rollinson & Jones, 2006). As common denizens of urban environments, magpies are routinely exposed to both anthropogenic noise and artificial light at night.

1.5 | Thesis Outline

This thesis consists of four empirical chapters which explore aspects of the hypothesised relationship between anthropogenic stressors, sleep, and cognitive performance in urban magpies (Figure 1.1). These chapters are aligned with two broad aims: 1) to determine whether exposure to anthropogenic noise affects cognitive development and performance in free-living and captive birds, and 2) to determine whether anthropogenic stressors such as noise and light at night might affect sleep. *Chapters 3 – 5* all conducted in captivity, a timeline of the captive experiments can be found in Figure 1.2.

In *Chapter 2*, I address my first research aim: investigating the effect of exposure to varying levels of naturally occurring anthropogenic noise on cognitive performance and development in urban magpies (Figure 1.1, Pathway 1). I used a battery of cognitive tests comprising four unique tasks, to test the cognitive capabilities of wild magpies occupying territories along an urban noise gradient. The tasks estimated performance of four cognitive abilities: *associative learning* (the ability to acquire knowledge through repeated experiences), *reversal learning* (cognitive flexibility, or the ability to inhibit previously learned behaviours), *inhibitory control* (the ability to supress an intuitive response) and *spatial learning* (the ability to remember the spatial location of rewards or threats). Using the same test battery, I compared the cognitive performance of juvenile magpies raised in territories of varying levels of noise through time (at ages 160 and 290 days post-fledging), to see if noise altered cognitive development.

Data gathering for *Chapter* 2 was conducted on free-living magpies in their natural habitat and therefore any effect of anthropogenic noise was potentially confounded by a variety of other variables associated with urban environments. To isolate the effect of anthropogenic noise, I studied how the cognitive performance of wild caught magpies was affected in captivity by exposure to experimentally controlled levels of anthropogenic noise (*Chapter* 3; Figure 1.1, Pathway 2). Using a similar battery of cognitive tests, I estimated the cognitive performance of birds exposed to playback of urban noise of realistic pattern and amplitude (a recording from an urban park in Melbourne), versus a quiet control. Magpies were exposed to playback for 21 hours a day for a two-week testing period. The playback was muted during testing (3 hours daily), enabling me to estimate pervasive impacts of noise on cognitive performance, rather than the immediate disruptive impact of performing under noisy conditions.

One of the hypothesised pathways by which anthropogenic pollutants might affect cognition is through disruption of sleep (Figure 1.1). Thus, my second research aim was to explore how exposure to two key anthropogenic pollutants: noise (*Chapter 4;* Pathway 3), and artificial light (*Chapter 5*; Pathway 4) might affect sleep in captive magpies.

In *Chapter 4*, I examined how exposure to urban noise influences the amount, composition, and intensity of sleep in captive magpies. I measured sleep by recording the EEG of wild-caught magpies before, during, and after exposure to 24 hours of recorded urban noise. The playback for the experiment was a novel recording, recorded in the same location as the playback as *Chapter 3,* and represented a realistic soundscape that magpies are likely to experience in the wild.

In *Chapter 5*, I studied the effect of artificial light at night on sleep. Again, I recorded the EEG of wild caught magpies and measured sleep before, during, and after 4 hours of exposure to light at night. Each bird was exposed to two different colours of lighting: white (blue-rich) and amber (blue-reduced), to determine if white light was more disruptive for sleep in birds than amber light (as has been noted in humans). Lights for this experiment were presented at ecologically relevant intensities, with illumination at intensities similar to those which magpies would experience in urban habitats.

Finally, in *Chapter 6*, I summarize the key findings and central conclusions of the thesis and offer suggestions for future research.

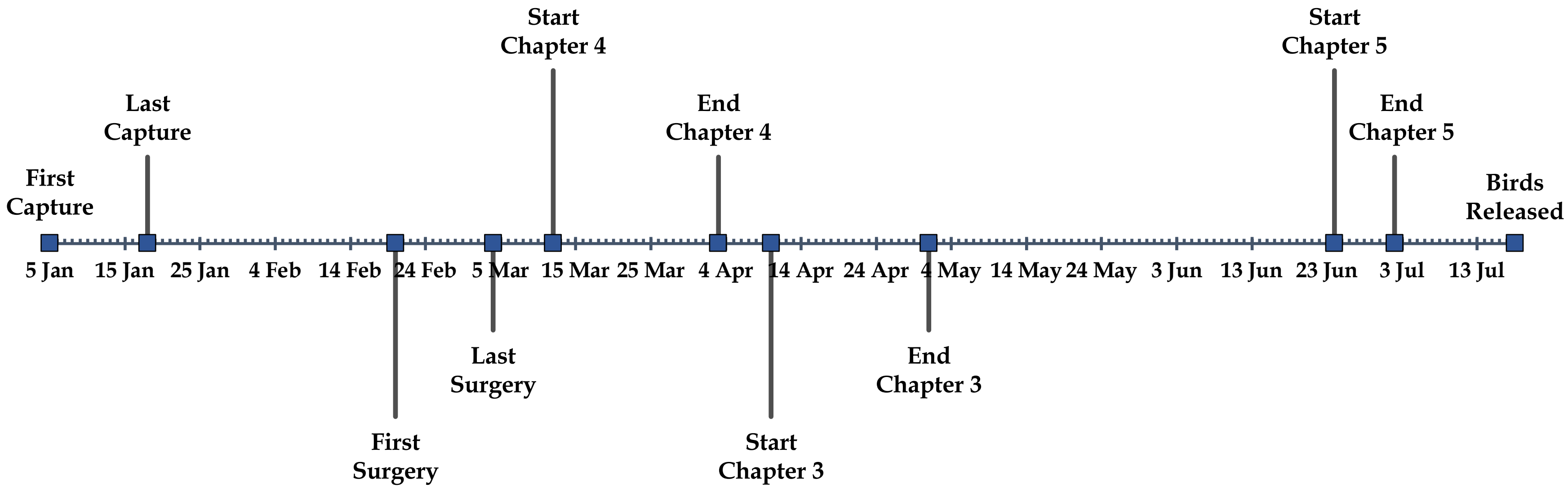

Figure 1.2. Timeline of captive studies. Birds were brought into captivity on 5th January 2019 and released on 15th July 2019.

Chapter 2 – Does anthropogenic noise affect cognitive performance in wild Australian magpies (*Cracticus tibicen*)?

Photograph: Juvenile magpie in front of an associative learning test board.

2.1 | Abstract

The expansion of cities and transportation networks has exposed much of the world to anthropogenic noise. This pervasive pollutant has a myriad of physiological and behavioural effects on wildlife. However, its impact on cognition remains unclear. To understand the cognitive consequences of anthropogenic noise, I measured differences in cognitive performance of an urban dwelling passerine, the Australian magpie (*Cracticus tibicen*) across a noise gradient. Utilizing a battery of tests to estimate several cognitive functions, I found no evidence that cognitive performance of wild Australian magpies varied in relation to the amplitude of ambient anthropogenic noise. Furthermore, with the exception of one function (spatial memory) the cognitive performances of adolescent magpies measured at two different developmental stages (average 160 and 290 days post-fledging) were similar, irrespective of exposure to relatively high, or relatively low levels of anthropogenic noise. Overall, these results suggest that levels of anthropogenic noise typical of city parklands do not have a strong impact on cognitive performance, but that noise may have the potential to impair the development of spatial memory.

2.2 | Introduction

Noise caused by human activity is rapidly changing Earth's natural soundscapes. Aircraft or vehicle noise can now be heard from some of the planet's most natural and protected environments (Buxton et al., 2017). How urban noise affects humans is relatively well understood, including severe health-related impacts like disturbed sleep (Frei et al., 2014; Halperin, 2014), hearing damage (Passchier-Vermeer & Passchier, 2000), cardiovascular disease (Fyhri & Aasvang, 2010), and stress (Basner et al., 2014). However, the effects of anthropogenic noise on wildlife have only recently started to be explored. Research has begun to shed light on the negative impacts of high-amplitude anthropogenic noise on wildlife, both terrestrial and aquatic (Kunc & Schmidt, 2019). In terrestrial animals, noise may be associated with decreased survival (Francis & Barber, 2013; Kight & Swaddle, 2011; Raap et al., 2017; Schroeder et al., 2012) and breeding success (Ernstes & Quinn, 2016; Potvin & MacDougall-Shackleton, 2015), increased stress responses (Chloupek et al., 2009; Kleist et al., 2018; Wright et al., 2007), altered frequency and timing of vocalizations (Fuller et al., 2007; Guo et al., 2016; Kight & Swaddle, 2015; Potvin et al., 2014), and interference with migratory paths (McClure et al. 2013; McClure et al. 2017).

While there is emerging insight into the behavioural and physiological impacts of anthropogenic noise, surprisingly little remains known about how noise might affect the development and performance of cognition, including learning, memory, behavioural flexibility, and executive functions. This omission is significant because of strong links between cognitive function and fitness. For instance, individuals from the same species that perform better on cognitive tasks show increased reproductive rates (Ashton et al., 2018; Preiszner et al., 2016). Human children exposed to environmental noise (i.e. planes, trains, and cars) showed deficits in speech, reading comprehension, and memory consolidation (Basner et al., 2014; Halperin, 2014). Likewise, in captive animals, noise exposure had a negative effect on short term memory in rats (Kight & Swaddle, 2011; Rabat et al., 2006) and long-term memory in developing captive zebra finches (*Taeniopygia guttata*; Funabiki & Konishi, 2003). In mice, noise affected learning, memory, and motor coordination (Jafari et al., 2018), and impaired cognitive development (Barzegar et al., 2015).

Whether such cognitive impacts translate to wild animals in noise-polluted urban environments remains unknown. Evidence has emerged for differences in cognitive performance between birds from urban and rural environments on a variety of tests: reversal learning tasks in common mynas (*Acridotheres tristis*) and great tits (*Parus major*; Cauchoix et al., 2017; Federspiel et al., 2017); foraging tasks in Barbados bullfinches (*Loxigilla barbadensis*) and house finches (*Haemorhous mexicanus;* Audet et al., 2016; Cook et al., 2017); and obstacle removal tasks in great tits (Preiszner et al., 2016). Consistent cognitive differences between animals living in noisy urban environments versus quiet rural environments are suggestive of potential impacts of noise. However, urban and rural environments differ in a broad suite of potentially confounding variables (e.g. artificial light and habitat quality) in addition to noise.

In this study, I explored whether wild Australian magpies (*Cracticus tibicen*) exposed to varying levels of urban noise across a major city also varied in cognitive performance and in the acquisition of cognitive skills. Australian magpies are iconic Australian birds and ideal study subjects for investigating this question as they are common, inhabit urban, noise-polluted areas, and can be trained to complete cognitive tasks in close proximity to humans (Ashton et al., 2018; Mirville et al., 2016; Rollinson & Jones, 2006). Using a test battery developed for magpies to determine the link between group size and cognitive abilities (Ashton et al., 2018), I quantified individual performance on four tasks, each challenging a different cognitive function: (a) associative learning (the ability to acquire knowledge through repeated experiences; Morand-Ferron et al., 2016); (b) reversal learning (cognitive flexibility; Bond et al., 2007); (c) inhibitory control (self-control, or the inhibition of immediate responses; Isaksson et al., 2018; Kabadayi et al., 2018; MacLean et al., 2014); and (d) spatial memory (the ability to remember the location of resources or threats; Emery, 2006). Performance on these tasks allowed for an estimation of the cognitive capabilities of the magpies, which I predicted would be negatively impacted by increasing urban noise.

2.3 | Methods

(a) Study species

The study population consisted of 45 Australian magpies from 23 groups. The Victorian subspecies (*Cracticus tibicen tyrannica*) breeds cooperatively and lives in stable group territories usually ranging from 2-5 adults (Kaplan, 2004). Most groups in the study population were comprised of a dominant male, a dominant female and a subordinate female. Groups cooperate to defend the territory and subordinates are known to participate in alloparental care (Kaplan, 2004), although this was not ubiquitous in this population. Juveniles remained in their territory for approximately one year, at which point they were forced to leave by the adults. This expulsion usually coincided with the start of the breeding season. In other sub-species, juveniles will remain with their natal group and help raise the next season's brood (cooperative breeding: this was only witnessed in 2 of 23 groups). For this study, birds of unknown age (not identified in the nest) were placed in two age groups: subadult (no or partial adult plumage; 0 - 2 years of age); and adult (full adult plumage; 2+ years old).

Magpies (n = 127) were captured using a manually triggered, baited walk-in trap, and banded for individual recognition. Magpies were banded with a three-digit PVC band and a numbered metal band supplied by the Australian Bird and Bat Banding Scheme (Authority No. 1405). Unbanded magpies were recognized via a combination of group composition, geographical location, and/or unique physical characteristics (i.e. a limp, damaged wing, or unique plumage; n = 78 magpies in 23 groups). I habituated all magpies to humans, allowing me to work in close contact with them. Shredded cheese was used as both a treat to habituate the magpies and as a reward for the cognitive tasks. I trained magpies to jump onto a scale, so that I could obtain accurate body mass data throughout the year. During capture, tarsus (dial callipers, nearest 0.1mm) and wing (blunt-ended ruler, nearest 1mm) measurements were taken. Using body and tarsus length I calculated Scaled Mass Index (SMI; Peig & Green, 2009), an estimate of the body condition of all captured magpies.

(b) Study Site

The study took place in Melbourne and Greater Geelong in Victoria, Australia (Figure 2.1) between January 2016 and July 2019. Groups were selected based on two factors: the ability to be habituated and to span a range of "noisiness" or sound level of territories represented by A-weighted decibels (dBA). Noise levels across territories ranged from 40 dBA to 65 dBA. The sites with the lowest levels of noise averaged between 40 and 45 dBA, equivalent to the sound of a library or refrigerator humming, while the loudest sites were between 60 and 65 dBA, equivalent to a toilet flushing or a busy restaurant. Using a NSRT Sound Level Logger (Convergence Instruments, Canada), I recorded noise levels (in dBA) at two or three geographically dispersed locations in each territory. Decibels were recorded every second over one weekend and weekday day (using sunrise/sunset as a starting point). A site's sound level is representative of its average equivalent continuous sound level over that two-day period. To determine the noise level experienced by nestlings during early development, sound level loggers were placed close to active nests, either at the base of the nesting tree or in an adjacent tree (within 10m of nesting tree). These recordings estimated the amplitude of noise experienced by the nestlings during early development.

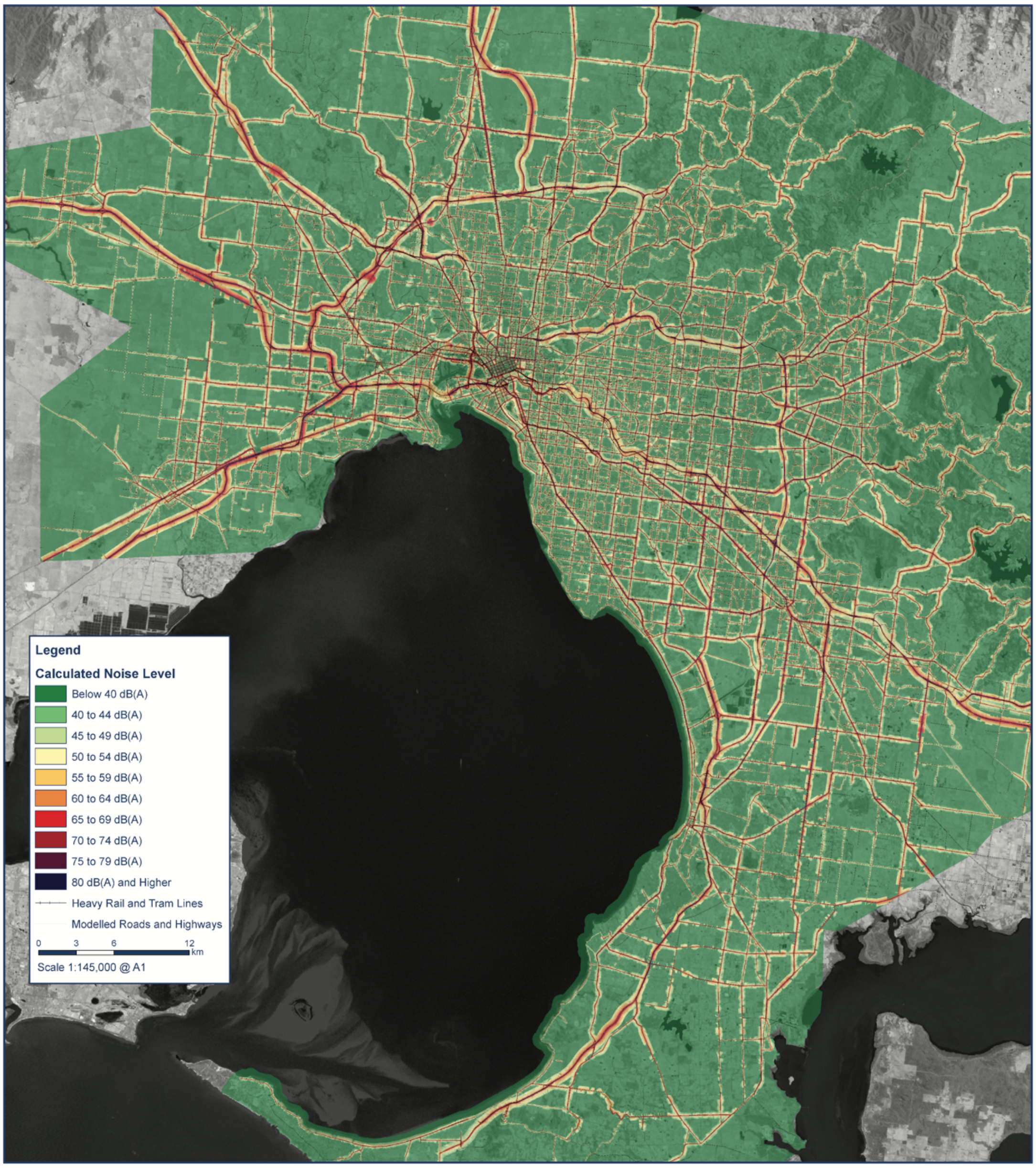

Figure 2.1. Anthropogenic Noise Map of Greater Melbourne, Australia. Data for road and rail noise levels (dBA) were collected in 2013 and 2014. Map was generated by EPA Victoria and VicRoads.

(c) Cognitive testing

To assess cognitive performance, 45 magpies (26 adults and 19 subadults) were presented with a test battery consisting of four tasks: (1) associative learning; (2)

reversal learning; (3) inhibitory control; (4) spatial memory. Tasks 2 and 3 represent executive functions, processes considered mechanistic or logically-based (Grafman & Litvan, 1999). Tests were presented in the order listed and details of each test are described below (see *Test Battery*). A new test began only once the previous test was completed. Isolation from other individuals was required during testing to avoid social learning. To achieve this, testing was temporarily suspended if another magpie approached to within 10 m of the focal bird being tested. I determined whether an individual was motivated to participate in testing by tossing a piece of cheese across its eyeline. If the bird flew in and ate the cheese, the test board was presented, and testing began. If the bird did not interact with the board for over one minute, the board was removed, and another piece of cheese was tossed to assess motivation. If the bird did not eat the cheese, testing would stop. Testing was never conducted on an unmotivated bird.

Prior to the start of testing, I used a motor skill task to train the magpies to interact with the test boards. This task consisted of a wooden block (30 cm long x 9 cm wide x 4 cm high) with four wells (3.0 cm deep and 3.3 cm diameter) drilled into it (Figure 2.1a). Each well was covered by a coloured plastic cap (a dark and light shade of yellow and green) held in place by a rubber band looped around nails set on either side of each well, which allowed the caps to rotate. By prodding the cap with their bills, magpies could flip the lid, expose the contents of the well and learn to access a food reward (grated mozzarella cheese) placed in the well. Magpies were presented with the training board until they were routinely accessing rewards from each well. Once successful, they moved onto the first cognitive task.

(d) Development

To test for longitudinal changes in cognitive performance through development, I presented eight magpies with the test battery (see *Test Battery*) at two different ages: mean 160 days (range: 133 – 219) and mean 290 (range: 270 – 344) days post-fledging. Testing began at 160 days post-fledging because at this age the magpies are beginning to feed independently and can easily be isolated from their parents and siblings for testing. At 160 days, juveniles were presented with the same test battery as the adults. Minor aspects of the task were modified (i.e. the colour of the caps for associative and reversal learning) between the 160 and 290 days to introduce novelty and test for genuine learning while allowing the comparison of scores (see *Test Battery*). The same protocol and criterion for success applied to the subadult and adult testing was used for juveniles at on average 160 and 290 days.

(e) Test battery

Associative learning -- I used a colour-discrimination task to test how quickly a magpie could associate a food reward with a novel coloured cap. This task utilised a similar testing block as the training stage, and therefore required no additional training. The foraging grid (19 cm long x 9 cm wide x 4 cm high) contained two wells (3.0 cm deep, 3.3 cm diameter; Figure 2.1b, c). Each well was covered with a cap of a different shade of the same colour (i.e. navy and sky blue;

violet and lilac purple). Shades were used instead of different colours in order to minimise any potential effects of colour preference (Ashton et al., 2018; Shaw et al., 2015). One well contained a cheese reward; the other well was empty. The colour of the rewarded cap was randomized. As in the training stage, shredded mozzarella cheese was used as a reward for a correct trial. In the first trial, magpies were allowed to search both wells in order to find the reward. In all consecutive trails, an incorrect choice (pecking the unbaited well) cued the removal of the board for one minute. Test subjects had a maximum of one minute to interact with the board before the board was removed from the testing area. The starting position of the food reward (left or right) was randomised and I avoided having the reward on the same side for more three consecutive trials. Cheese was wiped in both wells prior to the start of testing to prevent magpies from using olfactory cues to find the reward. The test was considered complete when the subject was able to select the correct well in 10 out of 12 consecutive trials (10/12 correct represents a significant deviation from random binomial probability; binomial test: $p = 0.04$; Ashton et al., 2018). If the bird did not complete the task (10/12 correct trials) in a single day the score would carry over to the next day and testing would continue with trials being added to the previous score. The total number of trials required to reach this criterion (including the final 12 trials) represented the associative learning score. At 290 days, juveniles were presented the same test; however, to maintain novelty, the colour of the caps were different (i.e. if birds had blue the first time they completed the test then they would be tested with purple the second time).

Reversal Learning – The reversal learning task was used to test cognitive flexibility, quantifying the number of trials required for a magpie to dissociate the previous association made and learn a new association, inhibiting previously learned behaviours. This task was presented the day after the completion of the associative learning task. The same test board was used (Figure 2.1b,c); however, for the reversal learning task, the shade of the cap covering the food reward was switched (i.e. associative food well = violet; reversal food well = lilac purple). The experimental protocol and completion criterion were the same as the associative learning task. At 290 days, juveniles were presented the same test but as described the cap colour of the food reward was switched.

Inhibitory Control – The inhibitory control task quantified a magpie's ability to inhibit a principal response and navigate around an obstacle to reach a reward. In this instance the principal response is to peck the plastic barrier to access the reward behind it. To measure this, I presented magpies with a 'detour reaching' task. In this task a food reward (mozzarella cheese) was placed inside a transparent open-ended cylinder (13 cm long x 5 cm diameter) mounted on a small wooden block (13 cm long x 7 cm wide x 5 cm high; Figure 2.1d). The cylinder was presented to the subject at a right angle to its body axis (open ends were positioned out of the magpie's eyeline), to see if it could solve the challenge of accessing the reward. As with the associative learning task, when first presented the detour task the subject was given time to explore the test board and find the food. Each trial thereafter counted towards their overall inhibitory score. In order to achieve a successful trial, the subject had to avoid pecking the closed walls of the cylinder and instead detour to the open ends and reach the food reward. Pecking the transparent cylinder counted as an incorrect score and cued the removal of the task for one minute. The task was considered complete when the subject correctly detoured the task three consecutive times. Magpies were allowed a maximum of 10 trials per day and trials were conducted in one-minute intervals. When possible, all trials were completed on the same day. At 290 days, juveniles were presented with a similar detour task, a transparent plastic 'wall' (30 cm long, 15 cm high) mounted vertically onto a wooden block (25 cm long x 9cm wide x 4 cm high; Figure 2.1e). The same methods and protocols were followed. I did not provide a training phase for this task as other studies have done, most often through the exposure of subjects to an opaque tube or wall prior to the transparent one (Kabadayi et al., 2018). This training phase was avoided because success on detour tests could arguably be linked to "a continued application of a learned rule" in addition to inhibitory control (Ashton et al., 2018).

Spatial Memory -- The spatial memory task was used to determine a magpie's ability to store important information regarding food placement and access it at a later date. The task consisted of a board (45 cm long x 27 cm wide x 4 cm high) containing a series of wells (3.0 cm deep, 3.3 cm diameter) to create a foraging grid (Figure 2.1f). All the wells were covered with lime green cap, the same colour used in the training board, and utilised the same flipping mechanism as the motor skill task so no additional training was necessary. Wells were numbered one through eight, front to back, starting with the left most well in the first row.

Each individual was randomly assigned a well number and that well contained the food reward for the entirety of the task.

Magpies were presented the test board five times over a 72-h period: twice on the first day, once on the second day, and twice on the third day. Each trial was deemed complete when the magpie found the reward well. The first test was the initial trial; magpies were presented with the board and allowed to search for the baited well. Once found, the boards were removed. After five minutes the same well was rebaited, and the training trial began following the same protocol. The third (24-h later) and fourth (48-h later) trials were presented the exact same way. The final trial, which controlled for olfactory cues (smell trial), was performed five minutes after the fourth trial. For the smell trial, the board was rotated 180 degrees and no reward was placed in the well. The foraging grid appeared identical to the subject, but the previously baited well was on the opposite side of the test board. This allowed me to determine if magpies used olfactory cues to find the location of the reward well. The total number of trials required to find the reward in the 24-h and 48-h trials determined a magpie's spatial score. At 290 days, the same methods and protocols were followed but a different well was randomly assigned to hold the reward.

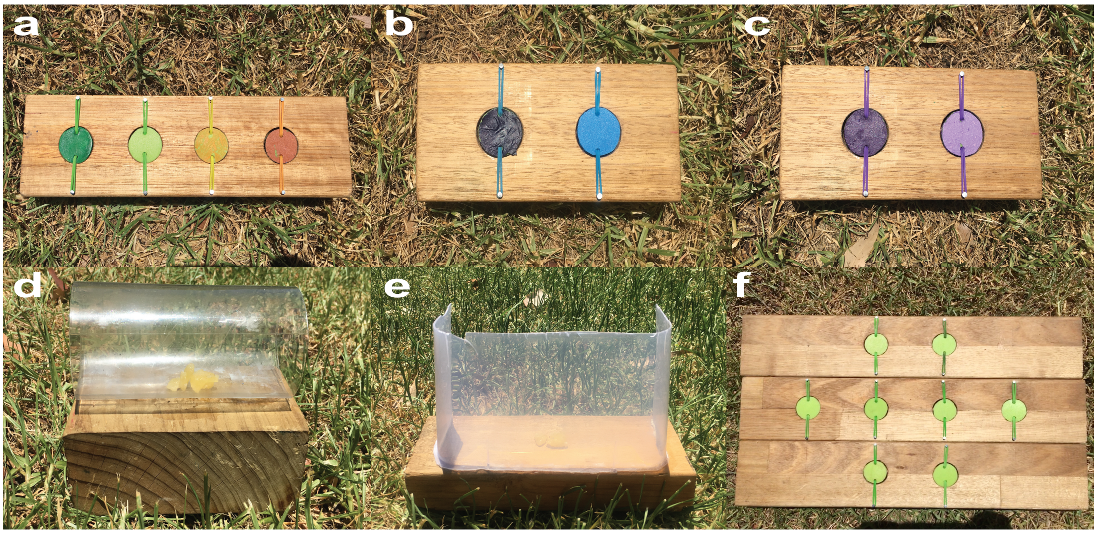

Figure 2.2. Cognitive Test Battery (a-d). The cognitive test series presented to individuals to quantify cognitive performance: (a) training board; (b, c) associative and reversal learning (purple and blue); (d, e) inhibitory control (cylinder: adult/subadults/age 160; wall: age 290); and (f) spatial memory.

(f) Statistical analysis

I conducted all analyses in the statistical environment R version 3.5.2 (R Development Core Team 2018). Using the R package lme4, I fitted generalized linear models (GLMM) with a Poisson error structure and logarithmic link to investigate variables affecting performance on all tasks. The GLMM contained all probable explanatory values: dBA, age, sex, SMI, and group size. Random effects included individual birds and the identity of the group the birds belonged to. I fitted a linear mixed effect model with the explanatory value decibels, controlling for group, to compare performance between the two development ages (160 and 290 post fledging) calculated as the proportional difference: (number of trials at 290 – number of trials at 160)/total number of trials at both ages. Due to the small sample size (n = 8), a linear mixed effect model was used instead of a GLMM. In addition, a paired t-test was used to determine if magpies used olfactory cues during spatial testing. All p-values for significant terms were obtained from these analyses.

(g) Ethics and permissions

All methods were performed in accordance with the guidelines and regulations of the University of Melbourne and were approved by the University of Melbourne Office for Research Ethics and Integrity, Animal Ethics (ID No. 1714094). Permission to capture, band, and test birds was granted by the Department of Environment, Land, Water and Planning (10008264) and the Australian Bird and Bat Banding Scheme (ABBBS number 1405).

2.4 | Results

Performance on the battery of cognitive tasks did not vary predictably in relation to anthropogenic noise (dBA), suggesting that birds inhabiting noisier urban environments did not suffer reduced cognitive performance. The best predictor of task performance was age, with adults performing better on two of the tasks (inhibitory and spatial) than subadults. In addition, territory dBA affected the change in performance of juveniles on the spatial memory task at 160 and 290 days of age but did not affect performance on the three other tasks.

(I) Effect of urban noise level and age on cognitive performance

In total, 45 birds completed at least one of the tasks. Not all birds completed each task owing to the absence of a bird prior to the completion of the test battery, usual via loss of territory or death. A subset of 12 birds completed a combination of tasks twice (four adults completed associative and reversal learning twice; eight subadults completed all tasks twice). There was no difference in performance on any of the tasks based on average noise levels within the territory: associative learning: $z = 0.91$, $p = 0.37$; reversal learning: $z = -0.18$, $p = 0.86$; inhibitory control: $z = -0.72$, $p = 0.47$; spatial memory: $z = -1.11$, $p = 0.27$ (Table 2.1; Figure 2.2).

The associative learning task was completed by all 45 birds (26 adults and 19 subadults; Figure 2.2). Adults averaged 27.8 ± 26.7 trials and subadults averaged 40.7 ± 36.0 trials before success ($z = 1.14$, $p = 0.25$; Table 2.1). The reversal learning task was completed by 43 birds (24 adults and 19 subadults). Adults averaged 50.1 ± 26.8 trials and subadults averaged 54.7 ± 33.2 trials ($z = 0.05$, $p = 0.96$). The inhibitory control task was completed by 37 birds (19 adults and 18 subadults). Adults averaged 8.3 ± 7 trials and subadults averaged 16.3 ± 14.1 trials ($z = 2.88$, $p < 0.01$). Finally, the spatial memory task was completed by 33 birds (17 adults and 16 juveniles). Adults averaged 6.1 ± 3.7 trials and subadults averaged 9.6 ± 7.2 trials ($z = 2.04$, $p = 0.04$). In the olfactory test, I determined that the chances of using olfactory cues vs randomly selecting a different well was not statistically significant ($t = 1.90$, $p = 0.07$).

Figure 2.3. Effect of sound level on cognitive performance on the test battery. A total of 45 magpies from territories spanning a range of sound levels (dBA), tested on one or more of the tasks within the test battery – associative learning (n = 45), reversal learning (n = 43), inhibitory control (n = 37), and spatial memory (n = 33). Performance on these tasks by each bird is shown here separated into two age groups: adults represented by black points and subadults by white points.

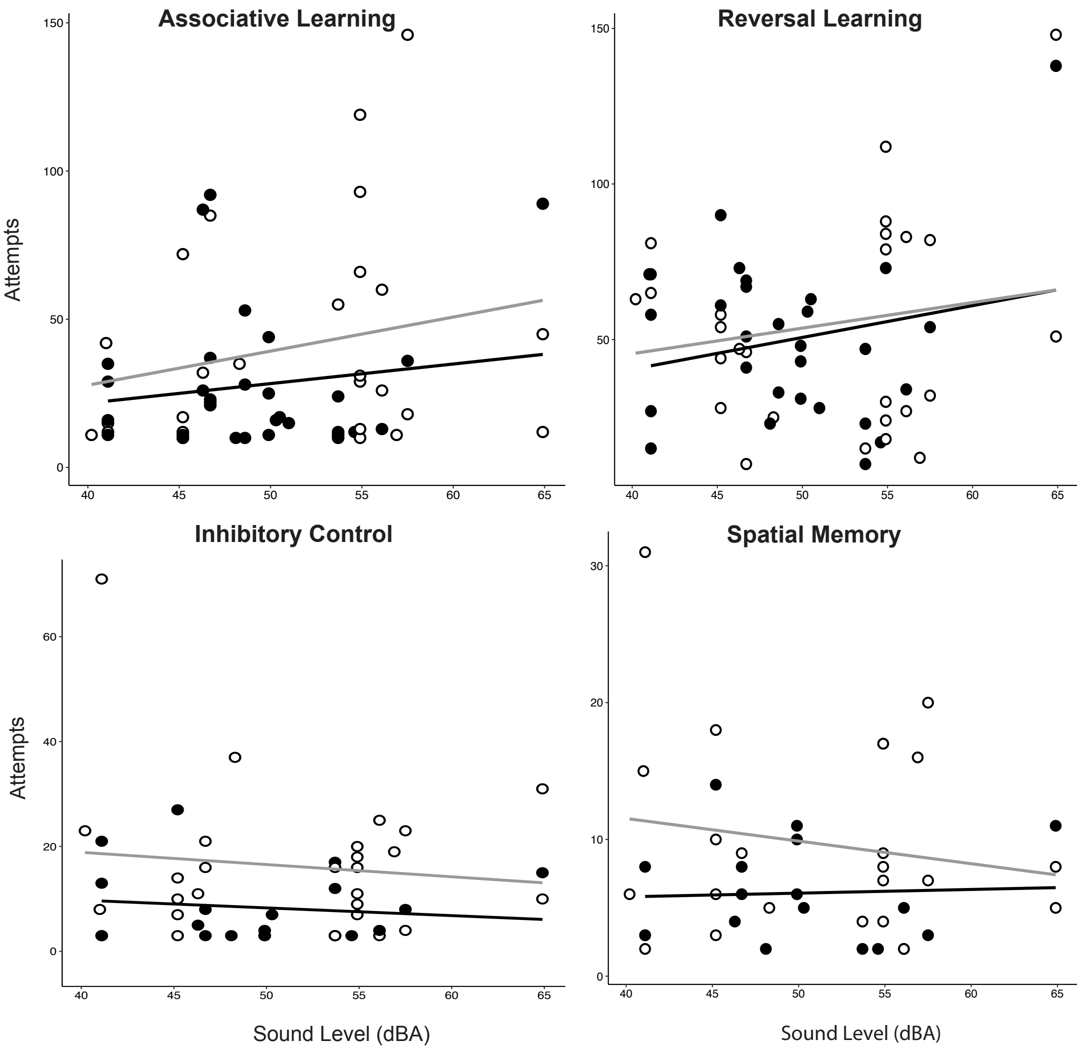

Table 2.1. Effect of sound level (dBA) on cognitive performance on the test battery. This table shows the GLMM analysis of the factors affecting performance (no. of trials to reach passing criteria) on all birds across all tasks – associative learning (n = 45), reversal learning (n = 43), inhibitory control (n = 37) and spatial memory (n = 33). Random effects included individual birds and their natal group. Data were fitted to a Poisson distribution with a logarithmic link function. Statistically significant results are highlighted in bold.

	Associative Learning			**Reversal Learning**		
Model Variables	**Estimate ± SE**	**z value**	***p* value**	**Estimate ± SE**	**z value**	***p* value**
dBA	0.02 ± 0.02	0.91	0.37	-0.002 ± 0.01	-0.18	0.86
age	0.34 ± 0.30	1.14	0.25	0.01 ± 0.20	0.05	0.96
sex (M/F/Unk.)	0.01 ± 0.34	0.03	0.98	-0.20 ± 0.24	-0.81	0.42
bsmi	0.001 ± 0.003	0.37	0.71	-0.003 ± 0.002	-1.04	0.30
group size	-0.25 ± 0.21	-1.22	0.22	-0.04 ± 0.15	-0.25	0.80
	Inhibitory Control			**Spatial Memory**		
Model Variables	**Estimate ± SE**	**z value**	***p* value**	**Estimate ± SE**	**z value**	***p* value**
dBA	-0.01 ± 1.56	-0.72	0.47	-0.02 ± 0.02	-1.11	0.27
age	0.81 ± 0.28	2.88	**<0.01**	0.56 ± 0.27	2.04	**0.04**
sex (M/F/Unk.)	0.08 ± 0.37	0.21	0.84	-0.07 ± 0.34	-0.20	0.84
bsmi	-0.002 ± 0.004	-0.65	0.52	-0.001 ± 0.005	-0.26	0.79
group size	-0.29 ± 0.20	-1.47	0.14	-0.09 ± 0.18	-0.50	0.62

(II) Effect of urban noise on cognitive development

Eight individuals completed all four tasks at both 160 and 290 days post fledging. Change in performance (proportional difference) on all tasks at 160 and 290 days was unaffected by dBA with one exception, spatial memory – association: t = -0.43 p = 0.68; reversal: t = -1.07, p = 0.35; inhibitory: t = -0.27, p = 0.80; spatial: t = 3.16, p = 0.02 (Table 2.2; Figure 2.3).

At 160 days, birds averaged 51.1 ± 44.4 trials on the associative learning task, 75.8 ± 42.0 trials reversal learning task, 24.8 ± 20.3 trials on the inhibitory control task and 11.8 ± 9.7 trials on the spatial memory task. At 290 days post fledging, birds performed significantly better on the inhibitory task averaging 6.1 ± 3.2 trials ($t = -2.5$, $p = 0.03$). No difference was seen on any of the other tasks at 290 days post-fledging, birds averaged 31.9 ± 29.6 trials on the associative learning task, 56.5 ± 19.4 trials on the reversal learning task, and 7.1 ± 5.9 trials on the spatial memory task.

Table 2.2. Analysis of the proportional differences in performance on the cognitive test battery by magpies (n = 8) at 160 and 290 days post fledging. I ran a linear mixed effect model to analyse the effect sound levels (dBA) have on the proportional differences in performance (performance at 290 days – performance at 160 days/total performance at both ages) on all tasks (associative learning, reversal learning, inhibitory control, and spatial memory) taking into account random effects (the group birds are in). Statistically significant results are highlighted in bold.

	Associative Learning			Reversal Learning		
Model Variables	**Estimate ± SE**	**t-value**	***p*-value**	**Estimate ± SE**	**t-value**	***p*-value**
dBA	-0.02 ± 0.05	-0.43	0.68	-0.04 ± 0.04	-1.07	0.35
	Inhibitory Control			**Spatial Memory**		
Model Variables	**Estimate ± SE**	**t-value**	***p*-value**	**Estimate ± SE**	**t-value**	***p*-value**
dBA	0.01 ± 0.03	0.27	0.80	0.10 ± 0.03	3.16	**0.02**

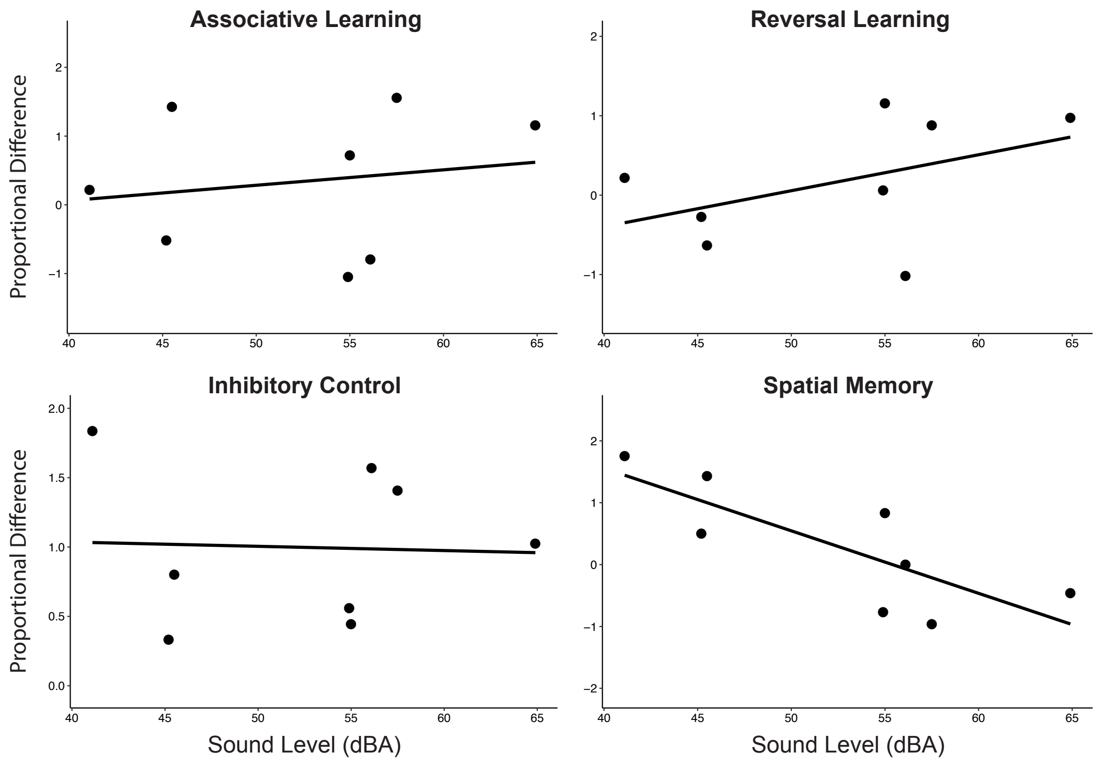

Figure 2.4. Proportional difference in performance on test battery between ages 160 and 290 days across a noise gradient. Magpies (n = 8) were tested twice during 2017 and 2018. The change in their performance on each test is represented by the proportional difference between the two testing ages: (performance at 290 days – performance at 160 days/total performance at both ages).

2.5 | Discussion

I found no evidence that cognitive performance of adult or subadult Australian magpies varied in relation to the amplitude of anthropogenic noise they were exposed to on their territories. Furthermore, with one exception (spatial memory) the cognitive performance of individuals measured at two different developmental stages (average 160 and 290 days post-fledging) was generally similar, irrespective of whether they had been exposed to relatively high, or relatively low levels of anthropogenic noise. This suggests that levels of anthropogenic noise typical of city parklands have the potential to affect development of spatial memory but not the other diverse cognitive functions.

How does urban noise affect performance on the test battery? Contrary to expectations, I found no effect of noise on cognitive performance on any of the tasks. Performance on associative and reversal learning showed a positive slope with higher sound levels (suggesting a tendency for deteriorating performance), while inhibitory control and spatial memory showed a negative slope (suggesting a tendency for improved performance). Age was the best predictor of performance on tasks, with adults performing significantly better than subadults on two of the four tasks (inhibitory control and spatial memory).

These results suggest that variation in anthropogenic noise has little or no effect on cognitive performance of either juvenile or adult magpies. While noise levels similar to the amplitudes found in my study population have been shown to effect reproductive success (Potvin & MacDougall-Shackleton, 2015), it is possible that deleterious impacts of noise on cognitive performance only occur at more extreme levels. Some studies exploring the impact of noise exposure on cognitive performance include noise levels above 70 dBA, also referred to as 'chronic' (Barber et al., 2010; Irgens-Hansen et al., 2015; Rabat et al., 2005); in a few cases, the study animals were exposed to noise levels with double the amplitude (10 or more dBA higher) of my loudest site. If my study sites were comparatively ‘quiet’, it remains possible that louder, ‘chronic’ sites might cause declines in performance on the test battery. In this study, such areas were either inaccessible (at airports or directly adjacent to freeways), lacked resident magpies, or included resident populations of magpies unaccustomed to human interaction, which could not be motivated to interact. Nevertheless, several studies suggest that the range across which I measured noise is fairly typical of urban environments. Potvin et al., 2011 found that over 99% of all ambient noise measured over more than 1 million km^2 of rural and urban habitats across south east Australia land was below 70 dBA. Thus, while habitats with chronic levels of noise exist (Kleist et al., 2018; Wolfenden et al., 2019) they are uncommon, and may not be representative of the conditions experienced by most urban wildlife.

As expected, adults outperformed subadults on the inhibitory and spatial tasks. In both humans and laboratory rodents, improvements on tasks, including inhibitory control and spatial memory, occur with increasing age and experience, as well as across adolescence and into adulthood (Ainge & Langston, 2012; Anderson et al., 2001; Meyer & Bucci, 2014). Studies on adolescent ravens (*Corvus corax*) also showed similar results, with behavioural elements of caching (a food storage behaviour displayed in many bird species that utilises spatial memory of which my task was based on) improving with age (Bugnyar et al., 2007). Adults did not outperform subadults on association or reversal learning. This could potentially be explained by the ease of associative learning, the difficulty of reversal learning, or the exploratory nature of subadult magpies. Birds are skilled at performing associative and discrimination tasks (Emery, 2006), and pigeons have been shown to discriminate between photos of other pigeons (Poole & Lander, 1971), cars, humans and flowers (Bhatt et al., 1988). While providing a measure of cognitive performance for which to compare magpies, associative learning does not represent a higher cognitive process and therefore may not be strongly impacted by age. In contrast, reversal learning is a complex task, that challenges an executive function, cognitive flexibility (Bond et al., 2007). It is possible that the reversal task I presented may be too difficult to be explained by age after only a single testing cycle. Research suggests that serial reversal tasks may provide a better measure of individual variation through the comparison of improving performances across successive reversals (Bond et al., 2007; Emery, 2006). Presenting the test in this fashion may have provided more insight into how age and other factors affect performance. In addition, subadult magpies may be less neophobic and possess exaggerated exploratory tendencies compared to adults. These traits may contribute to an individual's willingness to trial a novel task such as the ones presented and potentially perform better than a more reserved individual (i.e. an adult; Biondi et al., 2010; Greenberg, 2012; Kendal et al., 2005; Mirville et al., 2016).

How does urban noise affect cognitive development? The differences in performance on tasks by individuals measured at two timepoints was not correlated with higher sound levels, with the exception of spatial memory. Birds from habitats that routinely experienced higher sound levels performed worse on the spatial memory task at 290 days post fledging than 160 days compared to birds from habitats exposed to lower sound levels. In addition, birds performed significantly better on the inhibitory task at 290 days than at 160; performance on the remaining tasks was statistically indistinguishable, though all tasks trended towards improved performance (fewer trials required for success) at age 290 days post fledging.

The lack of any correlation between sound levels and performance on association, reversal and inhibitory was unexpected; however, its impact on spatial memory matches other findings in the literature. Cognitive declines in memory, including spatial memory, were observed in rats exposed to noise both early in life (Barzegar et al., 2015) and during later life stages (Hu et al., 2014). It is therefore possible that noise has a stronger impact on memory than it does on other cognitive functions. While potentially compelling, the sample of birds available to estimate this effect (n = 8) was relatively small, due to fledgling mortality and early departure of birds from their natal territory. To confirm this observation, a study testing more birds at two different points within the first year of life, especially in the habitats with 60+ dBA, may provide more insight into the effect noise has on the development of spatial memory. Outside of spatial memory, I saw no indication of a negative trend in performance with higher sound levels and it therefore seems doubtful that repeating this study using these tests even in habitats exposed to higher sound levels would yield different results. Taken together, these results suggest that exposure to anthropogenic noise has the potential to impact development of spatial memory but does not appear to impair the execution of other cognitive tasks in magpies.

Despite evidence that urban environments include many potentially disruptive environmental elements (e.g. light, noise, and chemical pollution), many species thrive in these habitats. Indeed, studies of certain species have reported comparable or better performance on cognitive tasks by urban individuals compared to their rural conspecifics (which are presumably exposed to lower levels of disturbance; Audet et al., 2016; Preiszner et al., 2016; Sol et al., 2012). Magpies possess many of the traits that have been proposed to enable species to prosper in highly urbanised environments (Kark et al., 2007): the ability to live and forage without fear in the vicinity of humans; the ability to exploit human-related resources such as food waste; and the ability to compete effectively with conspecifics because of large body size and behavioural flexibility. Melbourne city parks offer open fields for foraging, often surrounded by old growth trees providing abundant nesting habitat for magpies. Thus, magpies may be well-adapted to surviving and indeed flourishing in cities. While there is evidence for short-term impacts of anthropogenic noise on sleep in magpies (*Chapter 4*), such impacts may not be sustained. Ultimately, the fitness consequences of long-term exposure to noise will need to be quantified in magpies and other species in order to assess whether anthropogenic noise is merely an environmental annoyance, or a persistent disruptive phenomenon with long-term effects.

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Chapter 3 – Cognitive performance in captive Australian magpies is unaffected by urban noise exposure.

Photograph: Taylor, one of the female Australian magpies tested in captivity

3.1 | Abstract

Exposure to anthropogenic noise is associated with an array of deleterious effects to wildlife. Research on this topic has focused on the behavioural and physiological responses of animals to noise, with little work investigating potential links to cognitive function. To fill this gap in our understanding, I explored how an experimental broadcast of ecologically relevant noise affected the performance of captive, wild caught Australian magpies (*Cracticus tibicen*) on a series of cognitive tasks. Tests were conducted over two weeks, during which magpies were exposed to either an elevated urban noise playback or a quiet control. Unexpectedly, Australian magpies performed similarly on all four tasks in both the presence and absence of noise. These results suggest that extended exposure to urban noise does not impair cognitive performance. I found that prior experience with a given task had a strong effect on performance, with birds performing better on a task on their second trial. My findings suggest that under controlled experimental conditions, there is little evidence that exposure to environmental noise has sustained deleterious effects on cognitive performance.

3.2 | Introduction

Exposure to human-generated, or anthropogenic, noise in the environment is increasingly seen as an important conservation issue for a diverse range of species (Kunc & Schmidt, 2019). In the US, over 83% of all land, including some of the most protected and sensitive areas, is within one kilometre of a road and its associated traffic noise (Buxton et al. 2017). There is increasing evidence that there are negative impacts of noise on animals in both terrestrial and aquatic habitats (Kunc & Schmidt, 2019). Noise has been implicated in reduced breeding success (Ernstes & Quinn, 2016; Potvin & MacDougall-Shackleton, 2015), altered migratory paths (McClure et al. 2017; McClure et al. 2013), decreased survival (Francis & Barber, 2013; Kight & Swaddle, 2011; Raap et al., 2017; Schroeder et al., 2012), changes to the frequency and timing of vocalizations (Fuller et al., 2007; Guo et al., 2016; Kight & Swaddle, 2015; Potvin et al., 2014), and altering anti-predator behaviours (Barber et al., 2010; Meillère et al., 2015; Yorzinski et al., 2015).

Surprisingly, relatively little is known about the impact of increasing noise pollution on cognitive performance. Studies in humans have shown short term exposure to anthropogenic noise impairs attention in children (leading to reduced comprehension and spatial memory while exposed to noise), and disrupts sleep (leading to reduced cognitive performance; Barzegar et al., 2015; Elmenhorst et al., 2012; Kabadayi et al., 2018; Smith, 2012; Stansfeld & Clark, 2015; Szalma & Hancock, 2011). Similar findings have been reported in mice and rats, with long-term chronic noise exposure impacting memory and sleep following the removal of noise (Jafari et al., 2018; Rabat et al., 2006) and short-term exposure affecting spatial memory in the presence of noise (Hu et al., 2014). The effect of noise on sleep in wildlife is beginning to be understood (*Chapter 4*), but its effect on cognitive performance remains unknown.

Measuring variation in cognitive performance in wild animals is challenging (Griffin et al., 2015; Morand-Ferron et al., 2016; Shaw, 2017). Individuals must first be trained to perform cognitive tasks and, once trained, must be motivated to perform when called upon, thus limiting the tests that can be run and the species that can be studied (Shaw et al., 2015). Traditionally, cognitive studies on animals have focused on a single cognitive feature, such as tool use (Emery & Clayton, 2004; Hunt, 1996) or spatial memory (Balda & Kamil, 1992; Lewis & Kamil, 2006; Tello-Ramos et al., 2019). While such studies demonstrate that animals are capable of impressive cognitive feats, they are less useful as assays of an animal's full cognitive abilities (Shaw et al., 2015). In addition, performance on one cognitive task can be influenced by previous experience, motivation, or the relevance of the test to the species performing it.

In order to more accurately quantify cognitive ability, researchers have developed batteries of cognitive tests that allow performance in multiple cognitive pathways to be evaluated. Test batteries have been used extensively in the laboratory on mice (Galsworthy et al., 2005; Matzel et al., 2003) and primates (Amici et al., 2012; Herrmann & Call, 2012) and the use of such tests on wildlife, specifically birds, is a growing practice (Ashton et al., 2018; Boogert et al., 2011; Isden et al., 2013; Shaw et al., 2015).

To understand what effect long term noise exposure might have on cognitive performance, I brought 12 Australian magpies (*Cracticus tibicen tyrannica*) into captivity and measured how exposure influences several cognitive abilities, using an established cognitive test battery (Ashton et al., 2018). Australian magpies are large, common passerines found in most landscapes across Australia. Magpies are an ideal species to investigate changes in cognitive performance based on noise exposure: they are successful urban adaptors, often found living along roadsides or in city centres (areas of high levels of anthropogenic noise); they tolerate close interactions with humans (Rollinson & Jones, 2006) and can easily be trained to appear when called (Ashton et al., 2018; Mirville et al., 2016; *Chapter 2*); and they are capable of completing cognitive tasks in the wild including a similar test battery to the one used in this study (Ashton et al., 2018; *Chapter 2*).

The aim of this study was to compare the cognitive performance of individual wild-caught Australian magpies exposed to noise, relative to a quiet control, using a test battery validated for this species (Ashton et al., 2018).

3.3 | Methods

(a) Animals and housing conditions

In January 2019, I captured 12 wild adult Australian magpies (six males, six females, sexed based on plumage; Kaplan, 2004) in the City of Melbourne, Australia, using a walk-in trap baited with grated cheese. All magpies came from non-breeding, groups in urban parklands and were captured within 6 km of one another. Some of the birds came from within the same groups, however, as they were non-breeding, social floaters their history is unknown. Magpies were transported to an indoor aviary facility near La Trobe University (Bundoora Campus) where they were housed in two experimental rooms with similar configurations (three males and three females were placed in each room; Appendix A, Supplementary Figures, Figure A1). Magpies were kept in individual aviaries (1.8 m high x 1.8 m deep x 0.9 m wide) that 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, and two video cameras with infrared capabilities (the first was mounted above the 1.3 m rectangular perch where the birds regularly slept; the second on the door of the aviary). The door camera was pointed towards the front perch to record testing. Magpies were fed a mixture of minced meat and an insectivore mix (55 g; Wombaroo Food Products, Australia) once per day (approximately 0900 h). On test days, food was not provided until after the testing period (1130 h). Water was provided *ad libitum* in a large bowl, providing the magpies with a place to both drink and bathe. Aviary floors were covered in woodchips and, to provide enrichment, 15 - 20 mealworms were scattered daily throughout the woodchips allowing the magpies to forage. Rooms were temperature controlled (22 ± 5° C) and insulated from all external light. Room lighting (153 ± 18 lux) was set to a 12 h light (0600 – 1800 h), 12 h dark photoperiod (1800 – 0600 h). Night lights (average ~ 0.1 lux at sleeping perch) were placed in each room allowing the magpies to move during the dark photoperiod without harming themselves.

Magpies were initially afraid of humans, flying to the top perch upon entering the room, or frantically flying back in forth within the cage. Over the first month of captivity, daily interactions with the birds habituated them to my presence, allowing me to enter room without fear from the birds, and in some instances, I was able to feed birds by hand. Magpies also habituated to each other over the course of captivity, with individual rooms joining together in carolling. Weight loss was monitored throughout captivity to ensure health of birds.

Ten of the 12 magpies underwent surgery and were implanted with a 'head plug' that allowed for the collection of the brain activity data for a different experiment that was conducted prior to this one (see *Chapter 4*, *Methods, Recording sleep* for more information). One bird could not be operated on owing to a pronounced cardiac arrhythmia under isoflurane and one bird died during surgery. The 10 birds that underwent surgery were presented with a simple motor test before and after surgery to determine if the procedure altered cognitive performance; birds were able to perform the task following surgery.

(b) Experimental design

To determine if noise affects cognitive performance, I used a paired design to compare performance on a battery of cognitive tests, completed in the context of exposure to anthropogenic noise, and without noise (Figure 3.1). Half the birds (one room) received the noise treatment first, and the other half received the control first. The noise playback was started 48-h before testing began in both treatments. Birds were tested for 3-h each day, during which the playback was muted to prevent potential distractions by intermittent noise. Playback was switched off once all birds had completed the test battery, and birds had seven days to recover. Following the week-long recovery, the treatment assigned to each room was switched and the experiment began again.

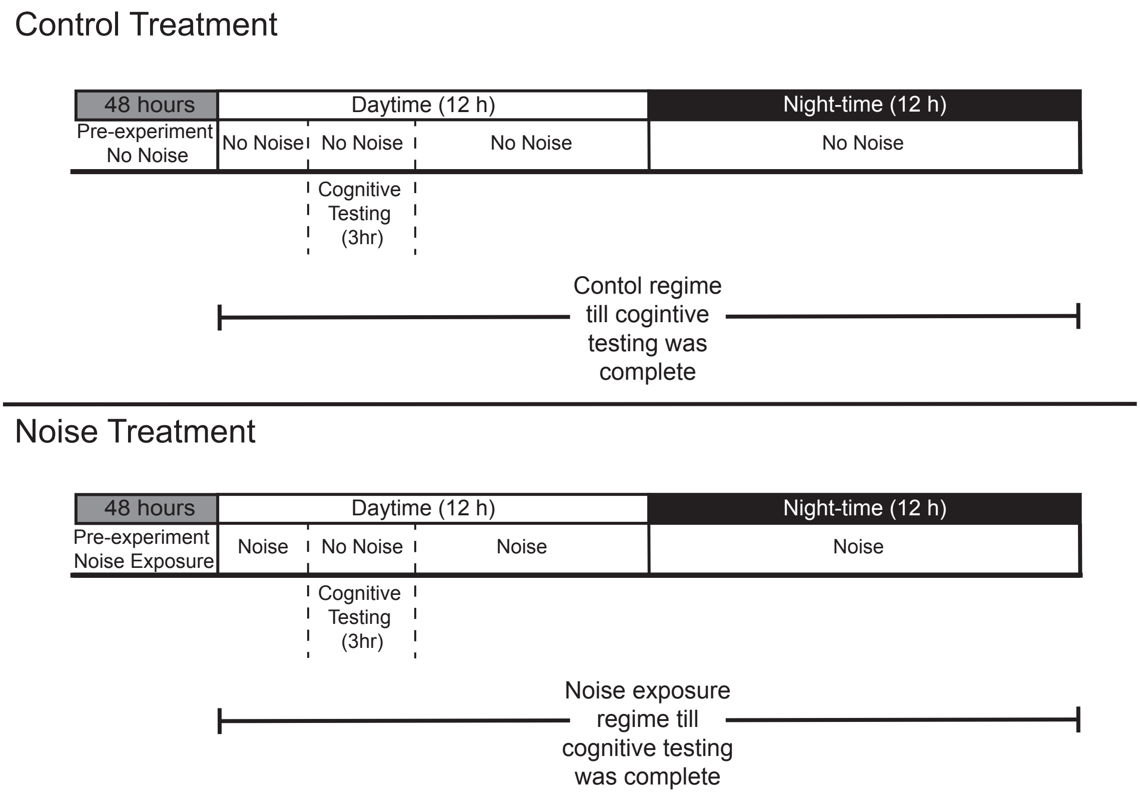

Figure 3.1. Experimental design and testing regime for (a) control and (b) noise treatment. Anthropogenic noise playback for the treatment began 48-h prior to the start of cognitive testing. Once testing began, noise playback was stopped for 3-h each day (0830 – 1130) to allow for silence during testing.

Noise playback -- For the noise treatment, I broadcast a recording of anthropogenic traffic noise for the entire 12-h night and 9-h each day during the weeks of the experiment (Room 1: April 8 – 20; Room 2: April 27 – May 9). Noise for the playback was recorded over one week (Monday-Sunday) at a busy roadside location in Parkville, Victoria, providing a realistic soundscape (sounds included cars, motorcycles, trams, people, dogs, and wildlife). The time signatures of the playback and the experiment were synced, and sunrise/sunset times mismatched by less than 15 and 50 minutes respectively; therefore, birds were experiencing realistic noises throughout each 24-h period. No behavioural differences were noticed between the treatment or baseline; foraging, carolling, and bathing behaviours were observed in both treatments. During the testing period (0830 h – 1130 h), the noise playback was muted (Figure 3.1). The treatment order was balanced and the room that started with the noise treatment was randomly selected. A single UE Boom 2 speaker (Ultimate Ears) was placed in the centre of each room to broadcast the playback for the noise treatment. These speakers would not accurately reproduce low frequency sounds or vibrations which could have additional effects on the birds. A sound level logger (Sound Level Meter Data Logger NSRT mk3; Convergence Instruments) was placed in each room, 3.5 m from the speaker, allowing me to measure the sound levels represented by A-weighted decibels (dBA) from a single point in the room throughout each treatment. The average dBA level of the playback over the testing period was 64 dB, with noise levels ranging between 40 and 90 dBA throughout each 24 h period (Appendix A, Supplementary Figures, Figure A2). The average sound level (64 dB) was well below the safe threshold for humans and within the range of noise pollution found in metropolitan areas (Brown et al., 2015). The background noise in the control treatment was 42 dBA, ranging between 42 and 63 dBA (Appendix A, Supplementary Figures, Figure A2), and composed of constant low-level noise generated by ventilation and air-conditioning systems, and high-level noise associated with magpie carols and calls. The difference in sound levels between the two treatments was statistically significant ($t = -38.2$, $p < 0.01$).

(c) Cognitive testing

Prior to the start of the experiment, I used a motor skill task or 'training board' to train the magpies to interact with the test battery. The training board consisted of a wooden block (30 cm long x 9 cm wide x 4 cm high) with four drilled holes (3.0 cm deep, 3.3 cm diameter) (Figure 3.2a). Covering the holes were four coloured plastic caps (two yellow and two grey). The plastic caps were held in place by a rubber band that looped around nails in the board. This set-up provided an axis by which the magpies could flip the lids. A few mealworms (3 - 5) were placed in each well as a reward. Magpies were presented with the training board until they were comfortably eating out of each well. The training board, as well as all other tasks, was positioned on the plank perch in the front of each enclosure for testing (Appendix A, Supplementary Figures, Figure A1).

I used a cognitive test battery to quantify differences in cognitive performance between noise treatments. Each magpie was tested daily and on average birds were presented a task two times per day. Birds took on average 8

± 2 days to complete all tasks. Testing was considered finished once all birds in each treatment had either completed all tasks or had ceased testing (three days of no interaction with a task). Treatment conditions in each room were then switched (i.e. birds tested in the noise control were now tested in the noise treatment), and following nine days of no testing, testing began again. Magpies were independently tested in their respective aviaries and curtains were hung in between cages ensuring testing occurred in isolation (Appendix A, Supplementary Figures, Figure A1).

The cognitive test battery consisted of five tasks. Each task tested a well-defined cognitive function likely ecologically relevant to Australian magpies: (a) Associative Learning – the ability to acquire knowledge through repeated experiences (Morand-Ferron et al., 2016); (b) Reversal Learning – cognitive flexibility (Bond et al., 2007); (c) Inhibitory Control (two tasks were used) – self-control, or the inhibition of immediate responses (Isaksson et al., 2018; Kabadayi et al., 2016; Kabadayi et al., 2018); (d) Spatial Memory – ability to remember the location of resources or threats (Emery, 2006). Tasks b) and c) represent executive functions (processes considered mechanistic or logically based; Grafman & Litvan, 1999). A new task could begin immediately after the previous task was completed, with one exception: reversal learning, which always started one day after the completion of associative learning task. The criteria for success varied between tasks, but in all tasks the total number of trials required to fulfil the success criteria acted as the test score; therefore, the fewer trials taken to reach their specific success criteria indicated a bird performed 'better' (see *Test Battery* for details). Performance on the test battery was used to compare individuals between the two treatments. Magpies were never forced to test; tasks only began when a magpie responded to a mealworm being placed in view by approaching and eating it. The training board was functionally identical to the associative learning, reversal learning and spatial memory tasks and therefore birds did not need to be further trained to operate those tasks.

Because birds were presented with each task twice in the paired design, minor aspects of the task were modified between the treatments to introduce novelty and test for genuine learning while allowing the comparison of scores (see *Test Battery*). For instance, in the associative learning task the colour of the caps covering the wells was blue for the noise treatment and purple for the control, thus providing a comparable test but with a novel colour.

(d) Test battery

Associative Learning – I used a colour-discrimination task to test how quickly magpies could learn to associate a novel coloured cap with a reward. The foraging grid (19 cm long x 9 cm wide x 4 cm high) contained two wells (3.0 cm deep, 3.3 cm diameter; Figure 3.2b,c). Each well was covered with a cap of a different shade of the same colour (i.e. navy and sky blue; violet and lilac purple). Shades of the same colour were used instead of different colours to minimize any potential effects of colour preference. One well contained a mealworm reward; the other well was empty. The colour of the rewarded cap was randomized. In the first trial, magpies were allowed to peck both caps in order to find the reward under the correct cap. In all consecutive trails, pecking the incorrect cap cued the removal of the board for one minute. Birds had a maximum of one minute to interact with the board before it was removed from the testing area. Testing resumed once the magpie showed interest in testing again. The position of the rewarded cap (left or right) was pseudo-randomized and I avoided having the reward on the same side for more three consecutive trials. The task was considered complete when the subject pecked the correct cap (and therefore the reward) in 10 out of 12 consecutive trials. 10/12 correct trials represents a significant deviation from random binomial probability (binomial test: $p = 0.04$; Ashton et al., 2018). If the bird did not complete the task (10/12 correct trials) in a single day the score would carry over to the next day and testing would continue. The total number of trials required to reach this criterion (including the final 12 trials) represented the associative learning score. To prevent olfactory cues, both wells were wiped with cheese prior to the start of testing. To maintain novelty, the colour of the caps was different for each treatment.

Reversal Learning – The reversal learning task was used to test cognitive flexibility, quantifying the number of trials required for a magpie to dissociate the previous association made and learn a new association (Figure 3.2b,c). Reversal learning utilized the same board as associative learning; however, the shade of the of rewarded cap was switched (i.e. if the reward cap was navy for the association learning task, it would be changed to sky-blue for the reversal learning task). The experimental protocol and completion criterion were the same as the associative learning task.

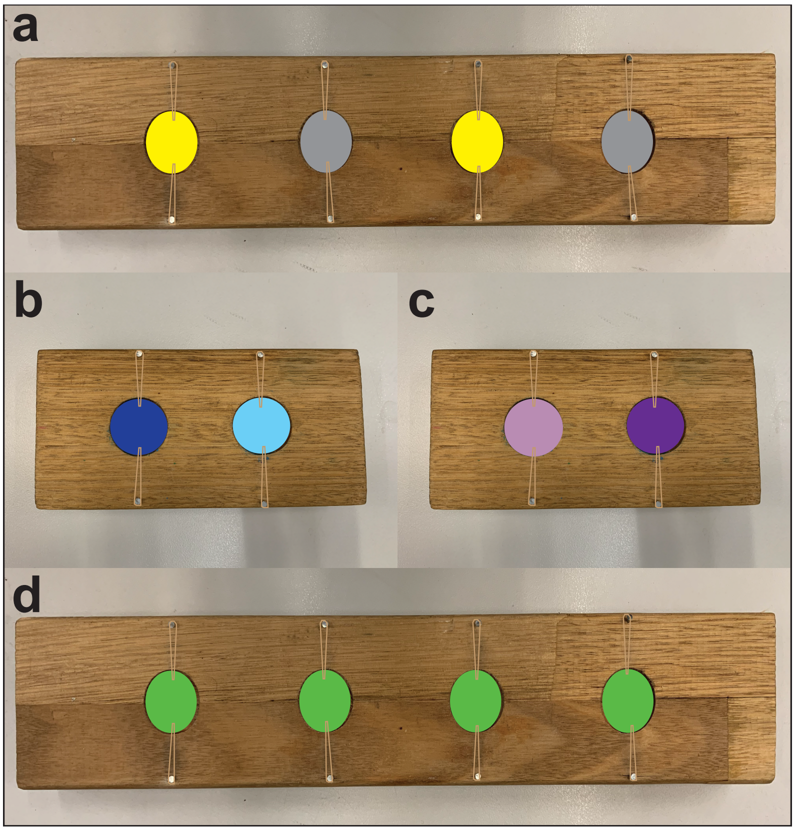

Figure 3.2. Training, associative learning, reversal learning, and spatial memory test boards. All these tasks utilized similar test boards: (a) training board; (b, c) associative and reversal learning (purple and blue); (d) spatial memory.

Inhibitory Control – The inhibitory control tasks quantified the magpies' ability to inhibit prepotent responses, and efficiently navigate around an obstacle to reach a goal (a food reward). In this instance, the prepotent response would be for the bird to trial to retrieve a reward by pecking at a transparent plastic barrier in front of a food reward. I presented magpies with two 'detour reaching' tasks, visually distinct but functionally similar. In the first task, a food reward (1-3 mealworms) was placed inside a transparent open-ended cylinder (13 cm long x 5 cm diameter) mounted on a small wooden block (13 cm long x 6.5 cm wide x 5 cm high) (Figure 3.3a). The cylinder was presented perpendicular to the subjects' body axis (open ends were positioned out of the magpies' eyeline), to see if it could solve the challenge of accessing the reward.

In the second inhibitory task, the cylinder was replaced with a transparent plastic wall (34 cm wide x 13 cm high) mounted vertically onto a wooden block (24 cm long x 9 cm wide x 4 cm high; Figure 3.3b). The reward (1-3 mealworms) was placed behind the wall. For both tasks, when first presented, the subject was allowed to explore the test board (i.e. cylinder or wall) and find the food. Each trial thereafter counted towards their overall score. A trial was considered successful if the subject did not trial to peck the closed side of the cylinder or the plastic wall, and instead walked either to the open ends of the cylinder or around the wall to obtain the reward. If the bird pecked the cylinder or wall, an incorrect score was tallied, and the test was removed from the testing area for one minute. The task was considered complete when the subject correctly detoured (without pecking) around the task to obtain the reward three consecutive times. Following established protocols (Ashton et al., 2018; *Chapter 2*) magpies were allowed a maximum of 10 trials per day on the detour tasks and trials were conducted in one-minute intervals (Ashton et al., 2018). When possible, all trials were completed on the same day. Test results for individuals on the two detour tasks were not statistically different ($t = 0.91$, $p = 0.38$) and therefore I tallied the number of trials taken to pass both these tasks into a single 'inhibitory score' per individual for the analysis.

After completion of the inhibitory testing, I presented the magpies with a 'control' task to determine if the magpies were actually inhibiting the urge to peck and not simply learning to avoid the barrier (an associative learning function). These tasks consisted of the same cylinder (Figure 3.3c) or wall (Figure 3.3d) but with a hole cut out of the centre of them, allowing the magpies to access the reward without detouring around the obstacle. A magpie completed a successful trial if they retrieved the reward through the cut hole instead of navigating around the obstacle. The success criteria were the same as for the inhibitory tasks.

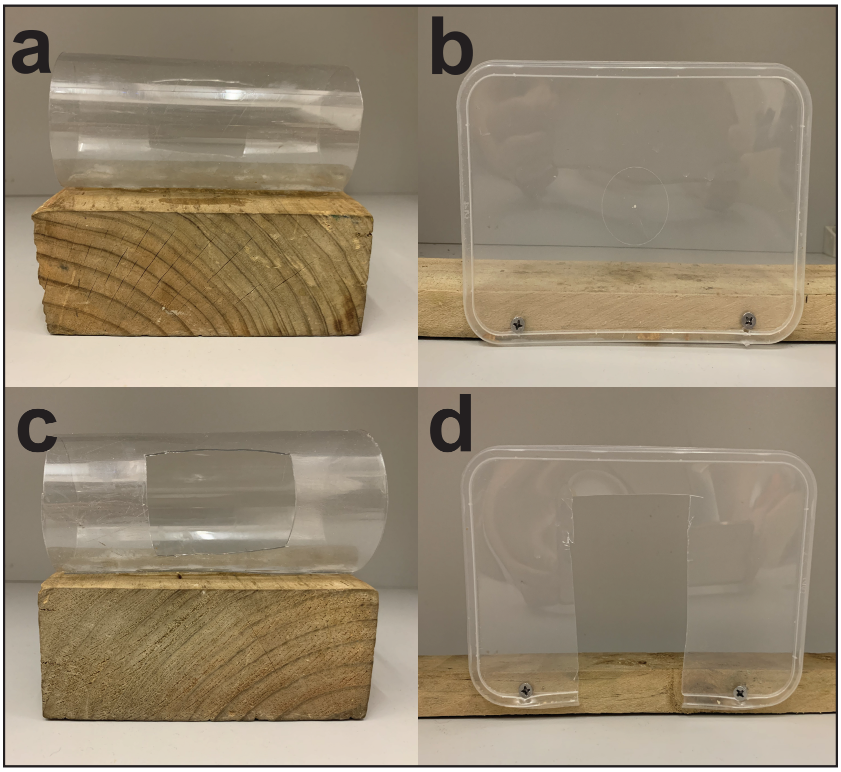

Figure 3.3. Inhibitory test boards. All inhibitory test boards: (a) cylinder detour task; (b) wall detour task; (c) cylinder control task; (d) wall control task.

Spatial Memory - The spatial memory task was used to determine a magpie's ability to store important information for later access. The task consisted of a wooden board (45 cm long x 9 cm wide x 4 cm high) containing an array of 1 x 4 wells (3.0 cm deep, 3.3 cm diameter; Figure 3.2d). This was modified from 2 x 4 x 2 well system used by Ashton and colleagues (Ashton et al., 2018) and in *Chapter 1* to better fit the physical constraints of the captive testing environment. Each well was covered with a lime green cap and utilized the same flipping mechanism as the associative and reversal learning tasks. Wells were numbered (1 - 4) from left to right. Each individual was randomly assigned a well number and that well contained the food reward for the entirety of the test. Magpies were presented with the test board five times over three days: twice on the first day, once on the second, and twice on the third. Each trial was deemed complete when the magpie found the rewarded well. The first trial was a 'baseline' trial. The magpie was presented with the board and allowed to find the rewarded well. Once found, the board was removed. After five minutes the same well was rebaited, and second trial or 'training' trial began, following the same protocol. The third and fourth trials were presented in an identical way, 24-h and 48-h later, respectively. The total number of trials required to find the food reward in the third and fourth trials determined a magpie's spatial score. To maintain novelty, the well assigned with the food reward was different for each bird in each treatment.

A final trial, the 'smell' trial, was performed five minutes after the fourth trial. For the smell trial, the board was rotated 180 degrees and no reward was placed in the wells. The foraging grid appeared identical to the subject, but the previously baited well was on the opposite side of the test board. This test was conducted to assess whether magpies might be using olfactory cues to determine the location of the baited well.

(f) Statistical analysis

I conducted all analyses in the statistical environment R version 3.5.2 (R Development Core Team 2018). Utilizing the R package lme4, I used generalized linear models (GLMM) with a Poisson error structure and logarithmic link to investigate the factors affecting performance on all tasks. The GLMM initially contained all probable explanatory values: treatment (noise or control), sex, treatment order (noise first or control first), test order (first trial or second trial), test type (associative learning, reversal learning, inhibitory control, spatial memory), body condition (SMI; Peig & Green, 2009) and the interaction between test order and treatment. Random effects included were individual birds and the room the birds were in. Terms were sequentially dropped from the model until a minimal model was established (treatment, test order, and sex). P-values for significant terms were obtained from the model. Paired t-tests were used to compare performances on individual tests.

(g) Ethics and permissions

All methods were approved by the La Trobe University Animal Ethics Committee (AEC 18034). Birds were captured and released with permission from the Department of Environment, Land, Water and Planning (10008264) and the Australian Bird and Bat Banding Scheme (ABBBS authority number 1405).

3.4 | Results

I found no difference in performance on any of the tasks under the control conditions compared to noise treatment, suggesting that exposure to noise did not affect cognitive performance (Table 3.1; Figure 3.4). However, birds performed better when they attempted a task for the second time, independent of the noise treatment.

Associative learning - Seven birds completed the associative learning task in both treatments, and an additional bird completed the task in only the control treatment but failed to interact with the task in the noise treatment. On average, individuals required 36.3 ± 20.0 trials to pass in the control treatment and 36.0 ± 19.9 trials in the noise treatment. The performance of all birds on the association task greatly improved the second time they performed it - first: 46.9 ± 15.0 trials; second: 25.2 ± 17.5 trials ($t = 3.68$, $p = 0.01$).

Reversal Learning - Seven birds completed the reversal learning task in both treatments. Individuals required 42.7 ± 30.0 trials to pass in the control treatment and 46.6 ± 31.5 trials in the noise treatment. Test order had less of an effect on the reversal task, with birds performing similarly on both test trials – first: 42.7 ± 27.6 trials; second: 46.6 ± 33.6 trials.

Inhibitory control - Nine birds completed both inhibitory tasks under treatment and control conditions. An additional bird completed the cylinder task in the control treatment but failed to interact with the cylinder task in the noise treatment, or the wall task in either the treatment or control and was thus not included in the analysis. Magpies averaged 11.4 ± 7.3 trials in the control treatment and 12.7 ± 12.1 trials in the noise treatment. Performance on the inhibitory tests was faster on average in the second trial than in the first, but the difference was not statistically significant – first: 14.6 ± 11.9; second: 9.5 ± 6.7 ($t = -1.40$, $p = 0.20$).

All nine birds completed both the cylinder and wall control tasks. There was little variation between the performance of birds on the control tasks in either treatments: cylinder – control = 4.5 ± 2.2 trials, noise = 4.8 ± 3.1 trials; wall – control = 4.4 ± 2.2, noise = 4.2 ± 1.4. Scores between the two tasks in each treatment were not statistically different (control: $t = 0.12$, $p = 0.91$; noise: $t = 0.60$, $p = 0.56$).

Independent of noise, birds successfully detoured around the cylinder task 65% of the time and the wall task 75% of the time, for an average success rate on both tasks of 70%. In the 'control' tasks, birds successfully retrieved the reward through the hole in the cylinder and wall control 85% of the time.

Spatial memory - Nine birds completed the spatial task in both treatments. Birds averaged 6.0 ± 2.9 trials in the control treatment and 5.0 ± 3.3 in the noise treatment. Test order did not affect the spatial task, with birds performing equally well on the task in both testing periods – first: 5.6 ± 3.7; second: 5.4 ± 2.6.

In the olfactory test, I determined that the likelihood of using olfactory cues was statistically indistinguishable from randomly selecting a different well ($t = 0.39$, $p = 0.77$).

Table 3.1. Effect of noise exposure on cognitive performance. GLMM analysis of the factors affecting performance (no. of trials to reach passing criteria) on all tasks considering random effects (bird and room). Data were fitted to a Poisson distribution with a logarithmic link function. Test type was not included in table. Statistically significant results are highlighted in bold.

final model	**Estimate ± SE**	**z value**	***p* value**
test order (first time testing/second time testing)	-0.29 ± 0.05	-5.53	**< 0.001**
treatment (control/high)	-0.06 ± 0.05	-1.18	0.24
sex (M/F)	-0.06 ± 0.31	-0.18	0.86

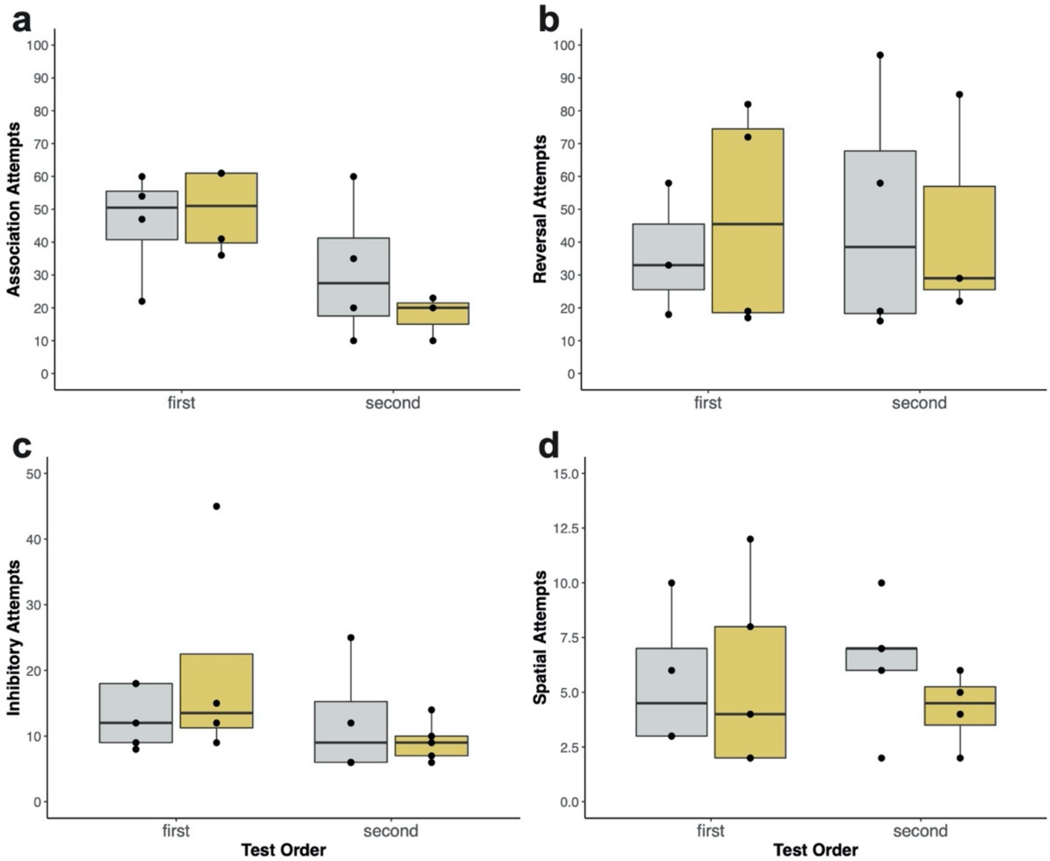

Figure 3.4. Effect of noise treatment on cognitive performance. The number of trials required to solve each task: (a) colour association, (b) reversal learning, (c) inhibitory control, (b) spatial memory. Scores are grouped by treatment (control: grey; noise: yellow) and test order (first or second).

3.5 | Discussion

Using a cognitive test battery, I found that Australian magpies performed similarly following exposure to noise and in the control, suggesting that extended exposure to urban noise does not affect cognitive performance. Prior experience with tests had the greatest impact on performance, with magpies showing improved scores on tasks the second time they were presented to them.

This provides evidence that magpies are able to learn from experience. Interestingly, birds performed differently on the two tasks that challenged executive function; improving performance on the detour tasks the second time presented but not on reversal learning. This discrepancy could be trivial, representing differences in scoring criteria; the two detour tasks had lower thresholds for passing compared to the reversal learning task. Alternatively, differing performances could indicate that these two tests were not equally complex or cognitively demanding. Reversal learning tasks are among the most widely used assays, and a staple in many cognitive batteries (Izquierdo et al., 2017). Likewise, detour tasks are common cognitive tests; however their use can be partially accredited to their relative practical ease in deploying and potentially less to their viability as a test of inhibition (discussed in detail below; Kabadayi et al., 2018; van Horik et al., 2018).

Cognitive performance was less affected by noise than I expected. There are several potential explanations for this result, including that immediate effects of noise are more important than long-term effects, that the effect was too small to detect without a large sample size, that physiological effects could be more important than behavioural effects, and that sleep loss may have affected cognitive performance.

First, to explore the possible impacts of noise on cognitive performance, I tested birds in identical conditions, silencing the playback during testing. As outlined in the methods, this was done to prevent distraction effects associated with the presence of anthropogenic noise. In an urban environment, noise is constant, and can affect birds both immediately (distraction, predator response, or territory defence) and over the long term (stress response, sleep deprivation). By muting noise during testing I sought to remove the short-term immediate effects, and instead look for sustained effects of long term noise exposure on cognitive performance. This design meant that I was not able to estimate the immediate short-term distractive effects of noise. Studies in humans have shown that environmental noise exposure can effect cognitive performance, and that removing the noise improves performance (Clark et al., 2013; Stansfeld & Clark, 2015). A future study, testing birds in the presence of background noise, may provide more insight into the immediate effects of noise on cognitive performance.

Second, for ethical and logistical reasons, the number of subjects used for this experiment was relatively small. In total, I was only able to obtain results for all cognitive tasks from seven birds and partial results from nine birds. Nevertheless, there was no indication of any consistent trend between cognitive performance and noise within my sample group and therefore there is no indication that a larger group would have given different results.

Third, I did not investigate differences between physiological and behavioural effects of noise, as I did not investigate blood chemistry. Magpies did not react well to people entering their enclosure or being captured; so, to prevent potential stress to the birds I did not collect blood samples. Noise has been shown to produce a stress response in birds (Kleist et al., 2018; Wright et al., 2007) and therefore it is possible that increasing corticosterone, a hormone in birds released in response to stress, may have caused changes in cognitive performance.

Finally, as per *Chapter* 4 exposure to noise disrupts and fragments sleep in magpies. Since sleep is directly linked to cognitive performance (Rattenborg et al., 2009; Samson et al., 2019), understanding how birds exposed to noise slept prior to testing may provide insight into the potential effect noise could have on cognition. A study looking at sleep the night before testing may show the impact medium term exposure has on cognitive performance.

In this study, I used two different detour tasks to investigate magpie self-control. The use of detour tasks as a reliable measure of inhibitory control has recently been called into question (Kabadayi et al., 2018; van Horik et al., 2018). It has been suggested that performance on these tasks may better represent an animal's previous experience with transparent objects or its general exploratory behaviour, rather than its ability to supress inhibition. Other studies also suggest birds may learn (continued application of a learned rule; Ashton et al., 2018) to go around a barrier instead of inhibiting a response (Kabadayi et al., 2018). To avoid this issue, all magpies were naïve to the transparent objects (cylinder and wall) when first presented. Magpies successfully detoured around both tasks 70% of the time, a score comparable to great tits (*Parus major)*, ravens (*Corvus corax*), and chimpanzees (*Pan troglodytes*), who all performed above 80% on similar tasks (Isaksson et al., 2018; Kabadayi et al., 2016), but who were all pre-trained and not naïve to their respective tasks. In addition, following the completion of the detour task, I presented them with a control task to test whether they applied a learned behaviour. Magpies quickly completed both control tasks, successfully eating the food through the provided hole 85% of the time. These two results provide further evidence that the inhibitory tasks I presented successfully challenged the bird's ability to inhibit a response, that magpies possess a high level of self-control, and through the use of a control task I present a method for testing inhibition in wildlife.

Performance on the spatial memory task was unaffected by both treatment and prior experience with the task. In fact, during the spatial task in both treatments, birds on average were no more successful at 24-h than at 48-h, selecting the correct well 26.3% of the time during both trials, almost equivalent to randomly selecting one of the four wells (25%). Birds did improve performance on the smell trial, selecting the expected well 42.9% of time, but this is still well below what might be expected from a bird that utilizes spatial memory for foraging (Balda & Kamil, 1992). These results call into question whether this task is suitable or relevant for magpies. While magpies have the ability to perform spatial memory tasks (Ashton et al., 2018; *Chapter 2*), there is little evidence that caching food is important to magpies in the wild. Spatial memory, often in the form of caching, is a behaviour in many wild bird species (Balda & Kamil, 1992; Lewis & Kamil, 2006). The majority of the magpie diet is made up of live prey and there is no indication that they store food for long durations. In addition, birds in the Southern hemisphere do not experience extreme winter conditions with low food availability that Northern hemisphere species do, potentially making caching a less ecologically important skill (Brodin & Urhan, 2014; Croston et al., 2017). While I have occasionally observed magpies caching food, they make little attempt to hide or camouflage items. In contrast, bird species that routinely cache employ sophisticated strategies to hide items from potential kleptoparisitism by conspecifics or heterospecifics (Brodin & Urhan, 2014; Bugnyar et al., 2006; Bugnyar et al., 2017). Corvids in particular are extremely efficient at caching (Emery & Clayton, 2004): Clark's nutcrackers (*Nucifraga columbiana*) are able to remember the locations of up to 30,000 seeds, while ravens alter cache locations based on the presence of potential pilferers (Bugnyar & Heinrich, 2006). I have never witnessed magpies exhibit such caching behaviours, or indeed retrieve food from a cache. Thus, it remains unclear whether this specific spatial memory task quantifies an ecologically relevant cognitive ability of magpies.

In sum, I found that exposure to a naturally realistic anthropogenic noise playback does not impair cognitive performance in Australian magpies, and that magpie performance was more affected by prior experience with a task; results consistent with findings in *Chapter 2.* This study also provides justification for testing magpies on associative learning, reversal learning, and inhibitory control, but suggests potential problems with testing them on spatial memory task. Magpies are urban exploiters (Diquelou et al., 2016; *Chapter 2*) that may benefit from the altering of natural landscapes by humans. Preferring fragmented forest habitats over densely forested areas (Kaplan, 2004), magpies thrive in city parks and sports fields, foraging not only on invertebrates in the soil but on food left by people. While there is evidence that noise has a negative impact on magpie sleep (*Chapter 4*), they may have a relatively high tolerance for noise (*Chapter 2*) and therefore may not display the negative impacts that have been documented in other species (Kleist et al., 2018; Potvin, 2017; Salmón et al., 2016). The rapid growth of the human population is quickly leading to expanding cityscapes within which urban exploiters such as magpies may be able to adapt and thrive.

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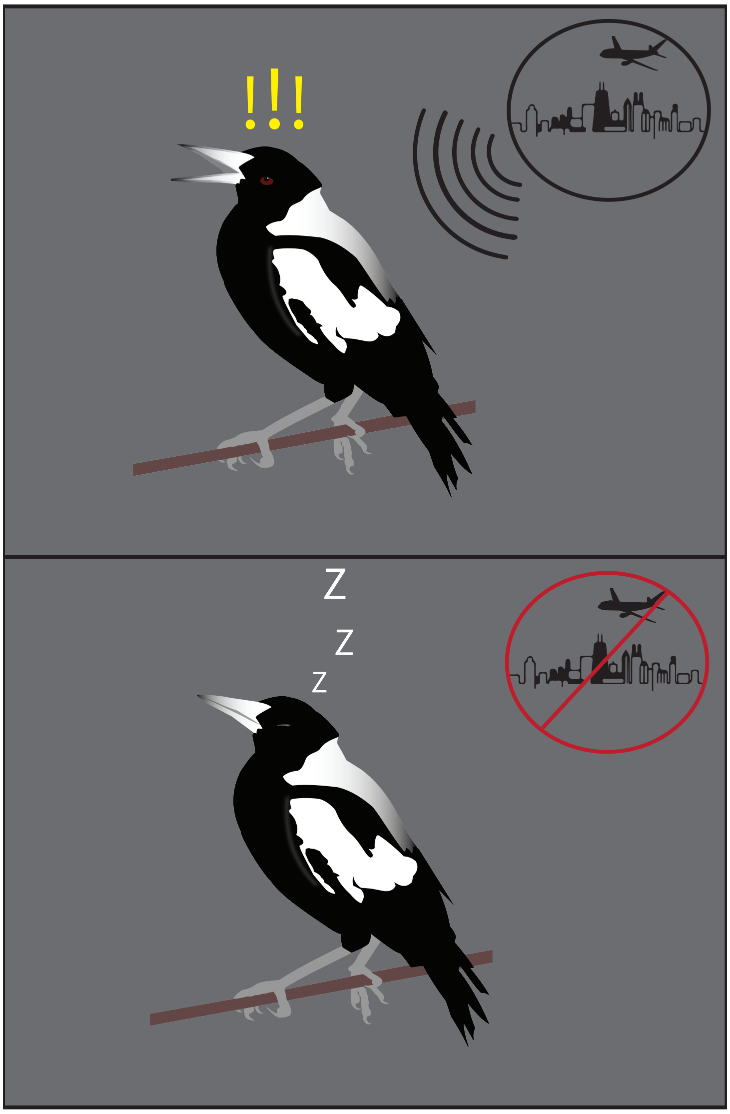
Chapter 4 – Urban noise restricts, fragments, and lightens sleep in Australian magpies



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4.1 | Abstract

Urban areas are inherently noisy, and this noise can disrupt biological processes as diverse as communication, migration, and reproduction. I 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.

4.2 | Introduction

Sleep serves many important and non-mutually exclusive functions. Sleep has been implicated in the maintenance of the brain (Fultz et al., 2019; Herculano-

Houzel, 2013; Tononi & Cirelli, 2016; Xie et al., 2013; Zada et al., 2019), improvements in attention, motivation, memory (Diekelmann & Born, 2010; Tononi & Cirelli, 2016; Van Dongen et al., 2003), and learning (Derégnaucourt et al., 2005; Huber et al., 2004), brain maturation early in life (Kayser et al., 2014; Scriba et al., 2013), and energy homeostasis (Schmidt et al., 2017; Siegel, 2009). The essential value of sleep is further implied by the apparent absence of any truly sleepless animal (van der Meij 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 (Aulsebrook et al., 2016; Ferretti et al., 2019; Lesku et al., 2012; Rattenborg et al., 2016).

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

I used behaviour and electrophysiology to investigate how experimental exposure to anthropogenic noise affects sleep in a native bird, the Australian magpie (*Cracticus tibicen*). 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, 2004). Utilizing miniature electroencephalogram (EEG) data loggers (Vyssotski et al., 2009), I recorded the electrical activity of the brain to provide insight into the amount, composition, architecture, 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 & Rattenborg, 2014; Vyazovskiy & Delogu, 2014). Furthermore, when birds and mammals are kept awake, they recover lost sleep by sleeping more, and by engaging in more intense non-REM sleep (Rattenborg et al., 2009; Tobler, 2011). Using these data, I was able to quantify any changes to sleep in wild-caught magpies exposed to urban-recorded, experimentally controlled noise in a laboratory context.

4.3 | Methods

(a) Animals and housing conditions

In January 2019, I captured 12 wild adult Australian magpies (equal numbers of each sex) in the City of Melbourne, Australia. Magpies were transported to an indoor aviary facility nearby La Trobe University where they were housed in two experimental rooms with similar configurations (Appendix B, Supplementary Figures, Figure B1). Room lighting (153 ± 18 lux) was set to a 12-h light, 12-h dark photoperiod (0700 h – 1900 h). All other details on animals and housing conditions were identical *Chapter 3* (see *Chapter 3*, *Methods, Animals and housing conditions* for more information).

(b) Recording sleep

To investigate the impact of urban noise on sleep, I implanted magpies with EEG and electromyogram (EMG) electrodes (1.5 – 2 months post capture; Figure 1.2). Briefly, magpies were anaesthetised with isoflurane (induction: 4-5%; maintenance: 1-3% vaporised in 100% O_2) using standard stereotaxic procedures. Five holes (0.5 mm diameter) were drilled through the exposed cranium to the level of the dura (membrane overlying the brain), without penetrating the brain. Four holes were drilled over the right hemisphere, located over four brain areas (hyperpallium, mesopallium, nidopallium caudolaterale [NCL], and cerebellum; the latter used as the reference). Electrode position was estimated based on (i) experience with other birds (Lesku et al., 2011a, 2011b, 2012; Tisdale et al., 2017), (ii) a brain atlas for a similarly-sized passerine (jungle crow, *Corvus macrorhynchos*; Izawa & Watanabe, 2007), and (iii) prior examination of the brain of a dead magpie and a pied currawong (*Strepera graculina*; belonging to the magpie family, Artamidae). It is possible that the NCL electrode was located on the *area parahippocampalis* – a thin veneer of the hippocampal complex overlying the NCL. A fifth hole was drilled over the left hemisphere for the ground. EEG electrodes consisting of gold-plated round-tipped pins (0.5 mm diameter) connected to medical grade electrode wire (AS633, Cooner Wire, Inc., USA) were placed into each of the five holes. EMG data were collected using two stainless steel wire electrodes placed on the neck muscle. All seven 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 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, I captured magpies by hand and connected an EEG/EMG datalogger (Neurologger 2A, Evolocus, Tarrytown, USA) powered by two zinc air batteries (ZA675 1.4V, Renata, Itingen, Switzerland) to the head plug. The datalogger was configured to continuously record the EEG and EMG, and included an inbuilt tri-axial accelerometer that measured head acceleration (ACC); all signals were sampled at 100 Hz. The logger 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.

Of the 12 magpies captured, I ultimately obtained complete data for 8 birds (five males and three females). One bird could not be operated on owing to a pronounced cardiac arrhythmia under isoflurane, one bird died during surgery, and technical problems with the dataloggers prevented collecting complete data from two other implanted birds. Data from these 8 magpies were collected between 12 March – 3 April. Two magpies repeated the experiment after a technical issue compromised data collection in the first instance; these magpies were given a minimum of one-week of rest between noise exposures. In addition, I failed to collect complete data from one bird: missing the recovery day and the second recovery night.

(c) Experimental design

Effects of recorded urban noise on sleep and recovery – I 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 hours) 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 (Appendix B, Supplementary Figures, Figure B2); 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. This sound level is well below the safe threshold for humans and is within the range of noise pollution found in 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 ± 6 dBA).

(d) Analysing sleep

To analyse the effects of urban noise on sleep I utilised the supervised machine-learning algorithm Somnivore™ to score wakefulness, non-REM sleep and REM sleep in 4 s epochs (a 4 s time period; Appendix B, Supplementary Figures, Figure B3). Somnivore has been validated previously for use on pigeons and has a high agreement with manual scoring (Allocca et al., 2019). Nonetheless, I validated Somnivore in this study for use on magpies by comparing four hours of manual scoring against four hours of Somnivore scoring during the baseline night: two daytime hours (*c*. 0100 h, *c*. 0800 h in circadian time) and two night-time hours (*c*.

1300 h, *c*. 2000 h) from eight recordings. The automated scoring of wakefulness, non-REM and REM sleep had high agreement with manual scoring: 99.4%, 97.0%, and 92.8%, respectively (overall 96.4%). Together with previous evaluations of Somnivore (Allocca et al., 2019), these results indicate that this software is effective at scoring sleep in birds.

A single scorer (R.D. Johnsson) 'trained' Somnivore by first manually scoring each recording with a minimum of 150 epochs of each state, dispersed over six hours (two during the day and four during the night). Manual scoring was completed by visually inspecting the EEG, EMG, and ACC channels and assigning a state to each of the 3 x 150 epochs. Wakefulness was characterised by EEG activation (small, fast brain waves) often accompanied by head movements (seen in the ACC and video recordings). As in other birds, wakefulness can also be identified by the presence of large amplitude artefacts in the EEG. Non-REM sleep was identified by large, slow EEG waves, accompanied by quiescent behaviour. REM sleep was characterised by a wake-like EEG pattern, but with no or very slow head movements (reflecting a head droop from REM sleep-related reductions in skeletal muscle tone); the EMG itself either showed a decrease, or no increase, from the preceding non-REM sleep level. Magpies generally slept with their heads buried in the feathers overlying their wings and back, so that their eyes were rarely visible. Consequently, I could not use eye state to help score sleep. After at least 150 epochs of each state had been scored, the machine-learning function of Somnivore was used to score all remaining epochs. The resulting scores were visually scanned to ensure that there were no systematic errors in the automated scoring (e.g. smaller non-REM sleep waves being mis-classified as wake or REM sleep). If errors were encountered, these were corrected manually, and Somnivore re-scored the recordings with the revised training.

(e) Statistical analysis

I conducted all analyses in the statistical environment R version 3.5.2 (R Development Core Team 2018). The data did not meet all assumptions for parametric testing, so I used paired t-tests to compare changes in the amount of each state across days, and the number and duration of state bouts between treatments when expressed as a 12-h daytime or night-time mean. I used a analysis of variance (ANOVA) to look for changes in sleep over time and across days.

To determine whether non-REM sleep intensity was influenced by urban noise, I calculated slow wave activity (SWA). SWA (typically 0.5 - 4 Hz spectral power density during non-REM sleep) 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 & 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, I 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 or 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. I used paired t-tests to compare the amount of SWA in each treatment per timepoint. Unless otherwise noted, the values presented in the results are means ± 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 released with permission from the Department of Environment, Land, Water and Planning (permit number: 10008264) and the Australian Bird and Bat Banding Scheme (ABBBS number 1405). 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, four birds were sighted one year after release, indicating no long-lasting effects of captivity or surgery.

(I) Magpie sleep composition

Baseline – Magpies are strongly diurnal (Figure 4.1). Magpies slept 10.8 h over the 24-h baseline day, and little of this (just 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 4.1). 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 ($F_{11,84} = 5.02$, $p < 0.01$), even if more of them ($F_{11,84} = 23.48$, $p < 0.01$). 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 (duration: $F_{11,81} = 4.15$, $p < 0.01$; number: $F_{11,81} = 19.87$, $p < 0.01$). 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 h – 1300 h). Magpie SWA during non-REM sleep declined significantly across the baseline night ($F_{3,28} = 2.95$, $p = 0.05$; see *Slow wave activity at night* below).

To better understand the sleep patterns of magpies, I also quantified total bout number and duration for each state (Table 4.2). During the night, magpies woke up 273 ± 27 times, and entered non-REM sleep and REM sleep 937 ± 20 and 698 ± 35 times, respectively. The similar number of sleep states 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 7 ± 0 s. During the day, the number of wake bouts were similar to the night (282 ± 61) but were considerably longer (200 ± 442 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), and thus daytime REM sleep was not analysed further.

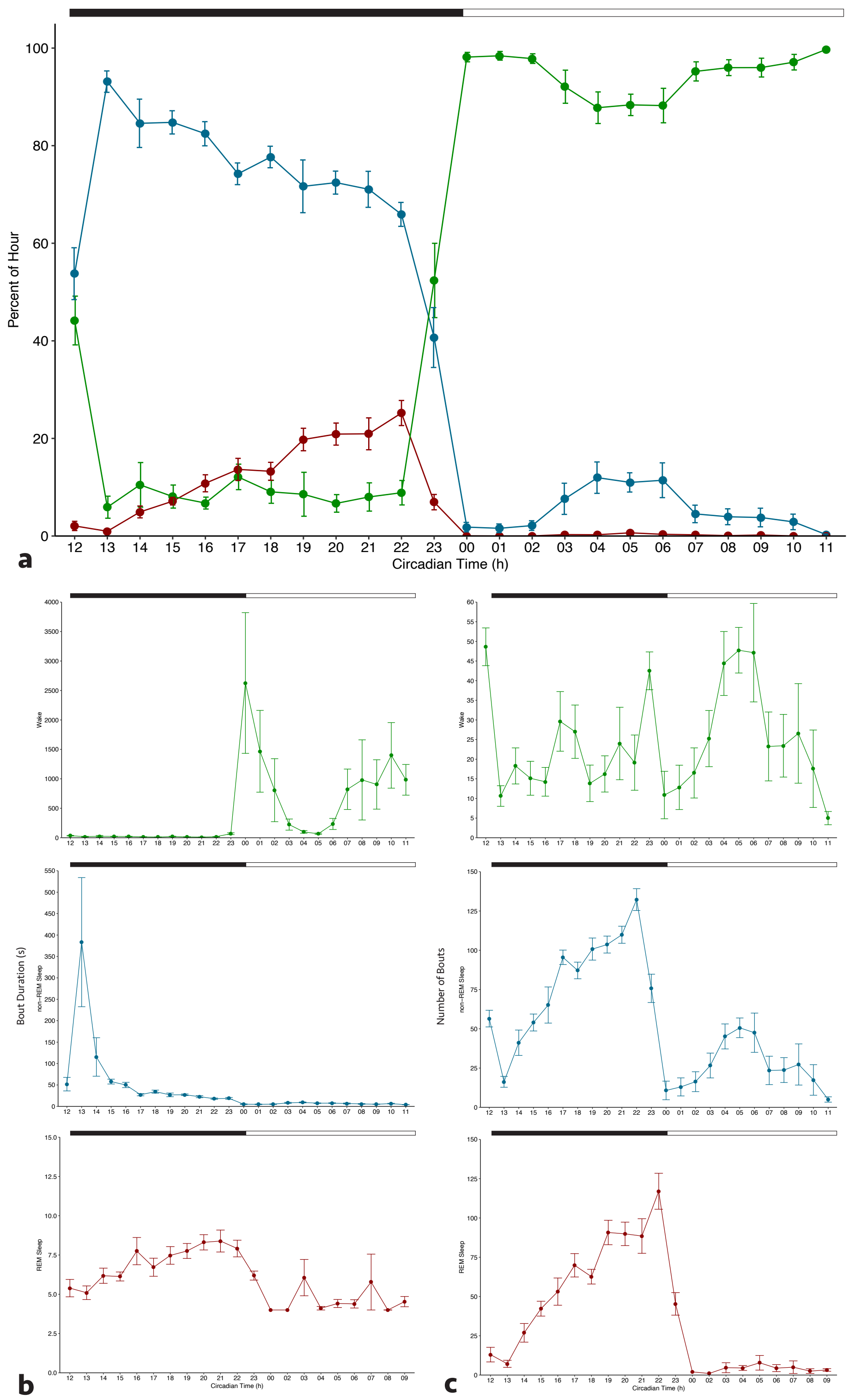

Figure 4.1. Magpie sleep architecture under baseline conditions. (a) Timing and amount (%) of wake (green), non-REM sleep (blue), and REM sleep (red) across the 24-h undisturbed recording, and the (b) duration and (c) number of state episodes. Time of day is expressed as circadian time, whereby lights 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.

(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. Under baseline conditions, magpies spent 15.1 ± 0.7% of the night awake, 72.7 ± 1.2% in non-REM sleep and 12.2 ± 1.0% in REM sleep (Table 4.1; Figure 4.2). In contrast, when exposed to noise, the time spent awake at night doubled to 32.8 ± 3.7% ($t = -4.26$, $p < 0.01$), non-REM sleep decreased to 61.6 ± 3.2% ($t = 3.28$, $p = 0.01$), and REM sleep was halved to 5.6 ± 1.3% ($t = 5.95$, $p < 0.01$). The percentage of night-time total sleep time allocated to REM sleep also decreased during the noise playback (baseline: 14.4 ± 1.2%; noise: 8.0 ± 1.7%; $t = 4.76$, $p < 0.01$). During 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 4.2).

Night-time sleep recovery – During the first recovery night, the amount of wakefulness decreased to 13.2 ± 0.6% compared to the baseline night (15.1 ± 2.0%; $t = 5.62$, $p < 0.01$), 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 unchanged ($t = -1.01$, $p = 0.35$; Table 4.1; Figure 4.2). On the second recovery night, no state differed from baseline (wake: $t = 1.19$, $p = 0.28$; non-REM sleep: $t = -0.93$, $p = 0.39$; REM sleep: $t = -0.05$, $p = 0.96$). During the first recovery night, there were fewer bouts of wakefulness, but the other architectural features of sleep were unchanged from baseline; on the second recovery night, there were again fewer bouts of wakefulness, and now non-REM sleep bouts were also fewer and longer, reflecting sleep consolidation (Table 4.2).

Table 4.1. 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	-

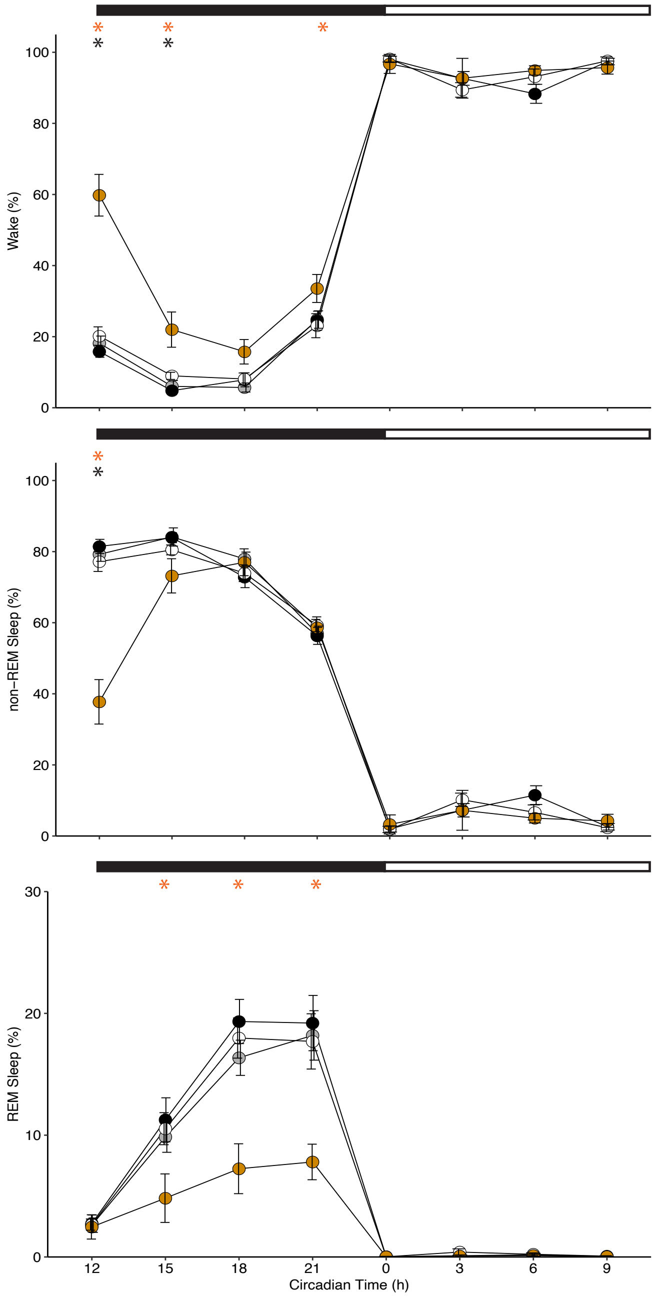

Figure 4.2. Effects of anthropogenic noise on the percentage of wakefulness, non-REM, and REM sleep. Data are summarised as quarterly (3-h) time bins for the baseline (open), noise treatment (orange; lasted the entire 24-h day), first (black) and second (grey) recovery days. Time of day is expressed 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.

Table 4.2: 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	-

Day-time sleep during noise playback – During the baseline day, magpies spent 94.6 ± 1.0% of the day awake, 5.2 ± 1.0% in non-REM sleep, and 0.2 ± 0.1% in REM sleep (Table 4.1; Figure 4.2). 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. During day-time exposure, duration and number of bouts of wakefulness, non-REM sleep, and REM sleep were all similar to baseline values (Table 4.2).

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 4.1; Figure 4.2).

Slow wave activity at night – SWA during non-REM sleep declined across the baseline night ($F_{3,28} = 2.95$, $p = 0.05$; Figure 4.3). In contrast, SWA during exposure to urban noise was low ($F_{1,62} = 29.52$, $p < 0.01$) and did not vary across the night ($F_{3,28} = 1.95$, $p = 0.14$). Over the first recovery night, SWA progressively declined ($F_{3,28} = 4.86$, $p < 0.01$), and was higher relative to baseline ($F_{1,62} = 3.90$, $p = 0.05$), reflecting non-REM sleep homeostasis. SWA during the second recovery night was not different from baseline values ($F_{1,54} = 0.51$, $p = 0.48$).

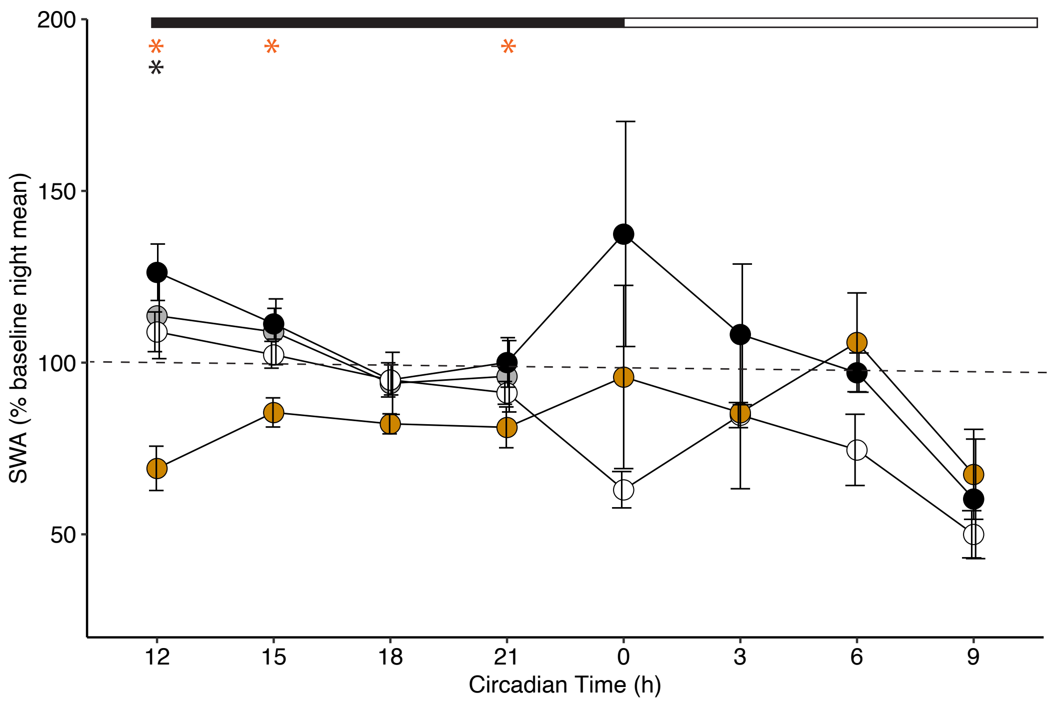

Figure 4.3. Effects of anthropogenic noise on non-REM sleep-related slow wave activity (SWA; 0.78 – 3.91 Hz power density). Data are summarised as quarterly (3-h) time bins for the baseline (open), noise treatment (orange; lasted the entire 24-h day), first (black) and second (grey) recovery days. SWA is expressed as a percentage of the baseline night non-REM sleep mean (i.e. the 100% dashed line). Circadian time plots lights on/off at 0/12 h, respectively; the horizontal bar along the top of the figure indicates photoperiod. 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.

Slow wave activity during the day – There was less than one hour of non-REM sleep across each of the 12-h days. Owing to the absence of much daytime non-REM sleep-related SWA data, variance during the day was greater than during the night (Figure 4.3). When the magpies slept during the noisy day, SWA was not different from baseline levels ($F_{1,47}$ = 2.87, p = 0.10). Conversely, SWA was higher during the recovery day than during the baseline ($F_{1,40} = 8.36$, $p < 0.01$), again reflecting non-REM sleep homeostasis.

4.5 | Discussion

I found that wild-caught Australian magpies, experimentally exposed to recorded urban noise in captivity, had restricted, fragmented, and lighter sleep. I provide evidence that lost non-REM sleep was recovered by sleeping more the following night, and more intensely night and day, when the playback was absent. I found no evidence for the recovery of lost REM sleep, which might challenge the widespread perception that this sleep state has an essential, restorative function. Overall, these findings provide, to my knowledge, the first experimental evidence that anthropogenic noise disrupts sleep in birds.

Magpies exposed to urban noise recovered lost sleep on the subsequent (quiet) 24-h day. This evidenced 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 and day. 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; Lesku et al., 2011a, 2012; Martinez-Gonzalez et al., 2008; Rattenborg et al., 2016; van Hasselt et al., 2019). Surprisingly, however, magpies did not experience a rebound in REM sleep. During noise exposure, magpies lost (on average) 47 minutes of REM sleep over the 12-h night, and throughout the two recovery nights, only gained back four of the lost minutes. While the absence of REM recovery has been shown in magpies before (Aulsebrook, Connelly et al., 2020), it remains unusual, as one would expect to see a REM sleep rebound fowing extended periods of wakefulness (Jones et al., 2008b; Lesku et al., 2011a; Martinez-Gonzalez et al., 2008; Rattenborg et al., 2009). Interestingly a recent study on starlings (*Sturnus vulgaris*) also found no evidence for REM sleep homeostasis following REM sleep loss (van Hasselt et al., 2019). Taken together, these studies challenge the presumed value of this sleep state. In any case, anthropogenic noise disrupted sleep in general, with the biggest effects on non-REM sleep intensity and the amount of REM sleep. The effect of urban noise on sleep did not persist beyond the first recovery day.

There are a variety of non-mutually exclusive mechanisms by which noise might have affected sleep in my study. First, particular sounds in the recorded noise may have triggered a behavioural response independent of sound amplitude *per se*. My 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) 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. I 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 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 my 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, my 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, I 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. The amount of sleep can differ between captive and wild animals (Rattenborg et al. 2008) and my 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 consequences for health, survival, and reproductive success given sleep's role in energy homeostasis (Schmidt et al. 2017), immune system maintenance (Imeri & Opp, 2009a; 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.

My findings suggest many avenues of future research. First, my 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 my 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 my experiment was a quiet environment, containing only the sound of an air conditioning unit. In nature, complete noiselessness is rare, and therefore my 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 anthropogenic 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 (Lesku et al., 2011a; Martinez-Gonzalez et al., 2008; 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 et al., 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 birds (Roth et al., 2006), as was the (short) duration of REM sleep bouts (Ayala-Guerrero et al., 2003; Lesku et al., 2011b; Rattenborg et al., 2004; Van Twyver & Allison, 1972).

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

Acknowledgements

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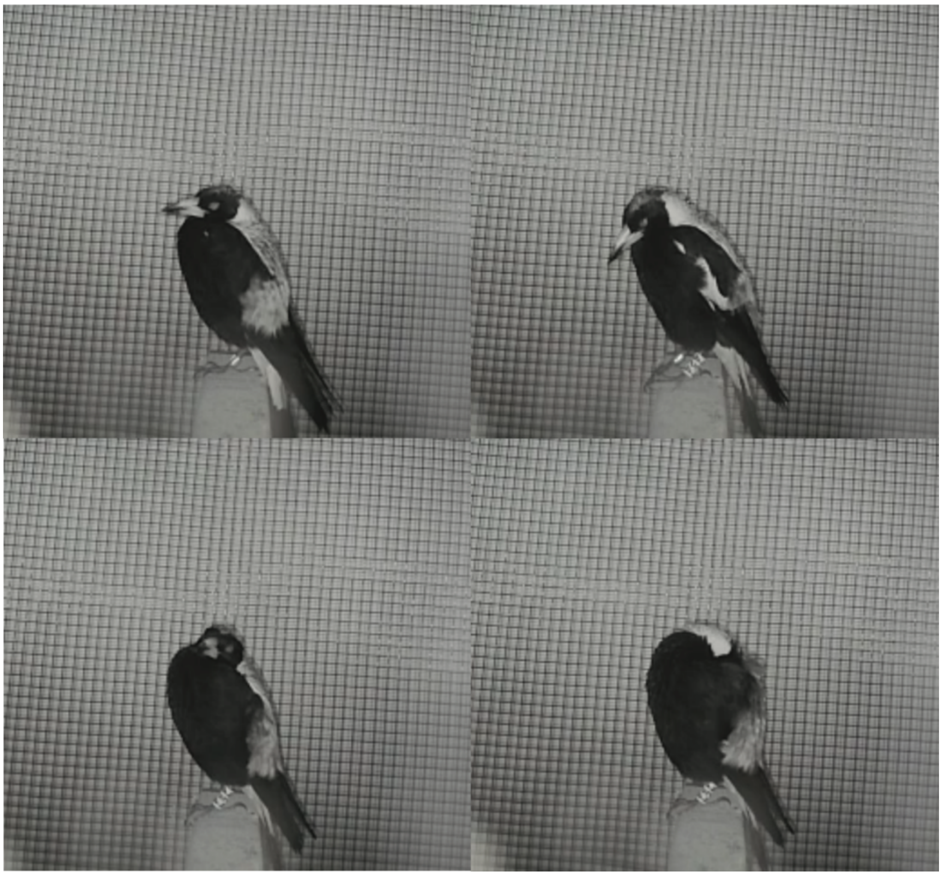
Chapter 5 – Waking up to the impacts of blue-rich lights: Australian magpies sleep more under amber light than blue



Video Stills: A series of behaviour sleep postures of an Australian magpie

Elements of this chapter are part of a compilation of several studies that is currently published in *Current Biology* as (*co-first author): Aulsebrook, A.E.*, Connelly, F.*, Johnsson R.D, Jones T.M., Mulder R.A., Hall M.L., Vyssotski A.L., and Lesku J.A. 2020. White and amber light at night disrupt sleep physiology in birds. Current Biology, 1-7.

5.1 | Abstract

Artificial light at night is becoming more prevalent in our natural spaces and has the potential to severely impact sleep in wildlife. Despite this, few studies have looked at the effect urban lighting has on sleep. I investigated the effect two different types of LED lighting has on sleep in a diurnal bird, the Australian magpie (*Cracticus tibicen*). Magpies exposed to 4h of ecologically relevant blue-rich and blue-reduced lighting during the night slept less and had more fragmented sleep. Following exposure, magpies recovered lost non-REM sleep by engaging in more non-REM sleep and by increasing its intensity. Birds showed no evidence for REM sleep homeostasis, failing to recover any REM sleep lost during exposure. In addition, I found that blue-rich lighting disrupted sleep more than blue-reduced lighting. These findings provide evidence that exposure to artificial light at night disrupts sleep electrophysiology in birds and, to my knowledge, the first experimental evidence that exposure to a part-night lighting disrupts sleep in birds (the impacts of which persist throughout the remainder of the night). Furthermore, these results show that white, blue-rich lighting disrupts sleep more than amber, blue-reduced lighting.

5.2 | Introduction

Sleep is an integral part of life and all animals appear to require sleep (Nath et al., 2017). The importance of sleep is further confirmed by its occurrence in the most dangerous of situations, including at the risk of predation (Lima et al., 2005) or while flying (Rattenborg et al., 2016). Sleep provides not only a means to rest and conserve energy (Schmidt et al., 2017) but serves many functions including promoting neural maintenance (Xie et al., 2013; Zada et al., 2019), health and survival (Imeri & Opp, 2009; Irwin, 2015), learning and development (Derégnaucourt et al., 2005; Kayser et al., 2014), and memory consolidation (Diekelmann & Born, 2010; Stickgold, 2005).

Sleep is regulated in part by the circadian clock (Aschoff, 1989; Kronfeld-Schor et al., 2017), which synchronizes sleep with the sun's light-dark cycle. However, over the past few decades, this clock has been recalibrated by the global proliferation of artificial light at night (Imeri & Opp, 2009; Kyba et al., 2017). Light at night can affect sleep physically, by supressing melatonin production (Dominoni et al., 2013), and behaviourally, by increasing anti-predator vigilance, foraging time, and activity patterns (Santos et al., 2010; Silva et al., 2014; Yorzinski et al., 2015). However, little is known about its effect on sleep architecture (Aulsebrook et al., 2018).

In birds and mammals, sleep is composed of two distinct sleep states, rapid eye movement (REM) sleep and non-REM sleep, and each is believed to serve a unique function (Vyazovskiy & Delogu, 2014). Measuring these states requires recording the electrical activity of the brain, visualised via electroencephalogram (EEG). Non-REM sleep is characterised by slow, large brain waves, and REM sleep is characterised by fast, small (wake-like) brain waves. Animals recover lost non-REM and REM sleep by increasing the amount of time spent in these states, and by increasing the intensity of non-REM sleep. Non-REM sleep intensity can be measured by the amount (or size) of slow waves during non-REM sleep (Rattenborg et al., 2009; Tobler, 2011). Few studies have quantified the direct effect of light at night on sleep composition and intensity outside of laboratory rodents and humans (Cho et al., 2016; Stenvers et al., 2016; Aulsebrook et al. 2018). Investigating the impact that exposure to light at night has on sleep in different species is necessary to fully understand the effect urban lighting has on wildlife.

While it seems likely that light at night can affect wildlife, mitigating it is challenging, as street and pathway lighting are unavoidable aspects of the urban environment. Efforts have been made to mitigate effects of urban light pollution in a variety of ways, including timed lighting, limiting illumination of pathways to trafficked times, and directional lighting (focusing lights specifically where they are needed and reducing excess 'bleeding' of illumination; Gaston et al., 2014). A more recently-proposed idea to eliminate some of the problems of urban light is to change the colour of lights (Longcore et al., 2018). Blue-rich lighting (wavelengths of 460 – 480 nm) has the greatest effect on melatonin production (Dimovski & Robert, 2018; Dominoni, 2015; Pandi-Perumal et al., 2006), a hormone that promotes sleep in animals (Gandhi et al., 2015), including humans (Ayaki et al., 2016; Santhi et al., 2012; Van Der Lely et al., 2015). Such results have led to recommendations that humans minimise their exposure to blue-rich light at night. However, recent discoveries provide contrasting evidence, suggesting that blue-rich and blue-reduced lighting equally impair sleep (Mouland et al., 2019). If changing the colour of urban lighting does not benefit wildlife, then alternative solutions to light pollution may need to be found.

I investigated the effect of four hours of exposure to two types of lighting, blue-rich (white) and blue-reduced (amber) lights, on sleep composition and intensity in captive Australian magpies (*Cracticus tibicen tyrannica*). This short-term exposure regime allowed me to compare the two light treatments and disentangle whether the impact on sleep was physiological or visual. If lights caused physiological effects, then I expected to see impacts on sleep both during and following the exposure. I predicted this would occur in magpies during blue-rich lighting exposure, as seen in humans (Ayaki et al., 2016; Van Der Lely et al., 2015). If lights caused visual effects, then I expected there to be an immediate disturbance to sleep during exposure and a quick recovery following lights being turned off.

Magpies are an ideal study species as they are commonly found in a variety of habitats, including brightly lit urban parks, and have a tolerance for close human interaction and captivity (Ashton et al., 2018; Mirville et al., 2016; Rollinson & Jones, 2006). Using miniature EEG data loggers (Vyssotski et al., 2009), I quantified sleep patterns and the effect exposure to white, blue-rich and amber, blue reduced light at night had on sleep composition, duration, and intensity in a population of captive magpies.

5.3 | Methods

(a) Animals and housing conditions

In January 2019, I captured 12 wild adult Australian magpies (equal numbers of each sex) in the City of Melbourne, Australia. Magpies were transported to an indoor aviary facility nearby La Trobe University where they were housed in two experimental rooms with similar configurations (Appendix C, Supplementary Figures, Figure C1). All other details on animals and housing conditions were identical to *Chapter 3* (see *Chapter 3*, *Methods, Animals and housing conditions* for more information).

(b) Recording sleep

To investigate the impact of artificial light at night on sleep I implanted magpies with electroencephalogram (EEG) and electromyogram (EMG) electrodes using standard stereotaxic procedures. For complete details on the surgery and how sleep was recorded see *Chapter 4*, *Methods, Recording sleep*. Surgery was performed more than three months prior to the start of the experiment, allowing time for the magpies to recover and become accustomed to the head plug.

(c) Experimental design

To investigate the impact of white and amber light at night on magpie sleep, I used a repeated-measures design that varied the presence and colour of light at night. I analysed sleep over an eight-day period. The first 24-h period (starting with night) functioned as the first baseline. The magpies were then subjected to four hours of dim (9.6 lux; Appendix C, Supplementary Tables, Table C1) light (either white, 4700 K or amber, 2190 K) from 1800 h – 2200 h followed by a further eight hours of darkness (lights-off), after which the night ended, and the lights came on again (Figure 5.1). The birds then had a total of 48-h of recovery under conditions identical to the initial baseline. This process was then repeated with the alternative light treatment colour, starting with a second baseline period. A total of seven birds were exposed to the white treatment first followed by the amber and seven birds were exposed to the reverse (amber then white).

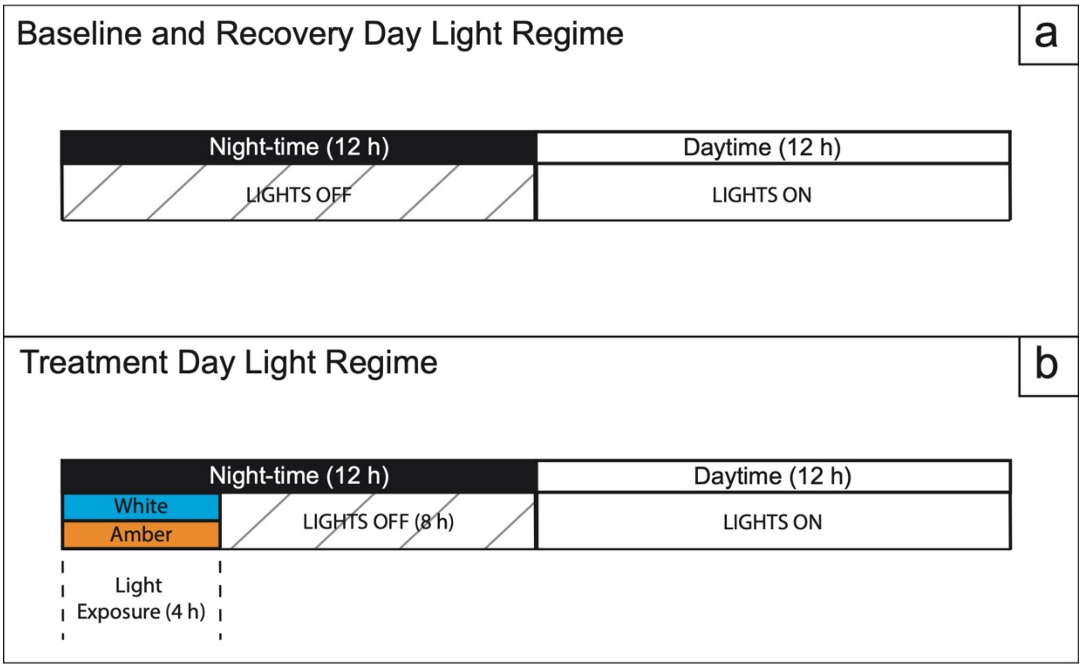


Figure 5.1. Light exposure light regime. Light regimes for (a) the baseline and recovery days, and (b) the treatment day (white, blue-rich and amber, blue-reduced).

The white and amber lights for each treatment were generated by a single 50 Watt LED super bright work light (Iron Horse Industries, LLC). Filters (LEE

Filters, Andover, England) were fitted to each light to produce the desired wavelengths and light intensity. To produce white lighting, I covered the LEDs with five white diffusion filters (416 Three Quarter White Diffusion filters). For amber lighting, I covered the LEDs with one amber filter (770 Burnt Orange filter) and two white diffusion filters, to match the light intensity of the white lighting. The lights were positioned in the centre of each room and projected upwards. Light intensity in lux was recorded from each enclosure at perch height inside each aviary. The light intensities used for the this experiment (9.6 lux) were based on measurements recorded near street lights in Melbourne urban parks, where wild magpies have been observed roosting and nesting (range: 0.06 – 19.7 lux). While light intensity in lux is based on human vision and thus may not represent what birds perceive, human perceptions of illumination are typically given precedence when designing and planning urban environmental lighting (Gaston et al., 2017). I therefore chose to measure light intensity in lux so that results from this research can be more easily transferred to real-world management contexts

Data were collected successfully between 24 June – 3 July 2019 from eight magpies (four males and four females): one bird died during surgery, another bird could not be operated on owing to a pronounced cardiac arrhythmia under isoflurane, and I was unable to collect complete data from two other (implanted) birds. Complete data were recorded for six magpies (four males and two females; two magpies (females) lost their loggers before completing the second light treatment and thus each received only one treatment (white and amber respectively). In total, complete data (i.e. baseline, treatment, and recovery) were recorded from seven magpies in each light treatment.

(d) Analysing sleep

To analyse the effects of urban noise on sleep I utilised the supervised machine-learning algorithm Somnivore™ (Allocca et al., 2019) to score wakefulness, non-REM sleep and REM sleep in 4 s epochs (see *Chapter 4, Methods, Analysing Sleep* for details on sleep analysis).

(e) Statistical analysis

I conducted all analyses in the statistical environment R version 3.5.2 (R Development Core Team 2018). I used paired t-tests tests to compare changes in the amount of each state across days, and the number and duration of state bouts between treatments when expressed as a 12-h daytime or night-time mean. I used a analysis of variance (ANOVA) to look for changes in sleep over time and across days.

To determine whether non-REM sleep intensity was influenced by artificial light at night, I calculated slow wave activity (SWA). SWA (typically 0.5 - 4 Hz spectral power density during non-REM sleep) 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 & 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, I 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 or transitions between states. SWA was calculated for each quarter (4-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. I used paired t-tests to compare the amount of SWA in each treatment per timepoint.

There were two baseline nights (one for each light treatment: white and amber) and therefore birds received the treatments in one of two ordered sequences. Treatment and recovery nights were always compared to the baseline night that preceded the specific light treatment night. T-tests were also used to compare order effects between the two light treatments. Unless otherwise noted, the values presented in the results are means ± SE (standard error).

(g) Ethics and permissions

All methods were approved by the La Trobe University Animal Ethics Committee (AEC 18034). Birds were captured and released with permission from the Department of Environment, Land, Water and Planning (permit number: 10008264) and the Australian Bird and Bat Banding Scheme (ABBBS number 1405).

5.4 | Results

Exposure to four hours of light at night affected both the amount and composition of night-time sleep. To explore this effect, I first separated each 12-h night (baseline, treatment, and recovery) into 4-h time blocks, representative of the four hours of white and amber light exposure. Daytime results are displayed in 12-hour blocks (baseline, post-treatment, and recovery) given the low values of daytime sleep, notably REM sleep.

(I) Effects of white light on sleep and sleep recovery

Baseline and treatment night – During the first four-hour block of the baseline night, magpies spent 11.7 ± 2.1% of the time awake, 85.0 ± 2.1% in non-REM sleep, and 3.3 ± 0.4% in REM sleep (Table 5.1; Figure 5.2). Magpies slept the most during the middle of the night (second four-hour block) spending 6.1 ± 0.8% of the time awake, 80.1 ± 1.7% in non-REM sleep, and 13.9 ± 1.7% in REM sleep. In the final four-hour block of the baseline night before lights on, magpies spent 17.7 ± 3.1% of the time awake, 61.2 ± 2.2% in non-REM sleep, and 21.1 ± 1.9% in REM sleep.

The following night, birds were exposed to four hours of white light at the start of the night. During the four-hour block of white light exposure, sleep composition was significantly altered compared to the same time period of the baseline night (Table 5.1; Figure 5.2). Time spent awake greatly increased ($t = -9.44$, $p < 0.01$), while non-REM sleep ($t = 9.42$, $p < 0.01$) and REM sleep ($t = 6.66$, $p < 0.01$) decreased. After four hours, lights were turned off and birds had eight hours of darkness before lights-on at 0600 h. During the first four-hour block of darkness after light exposure (temporally matched to the second four-hour block of the baseline night to account for circadian timing), birds spent more time in non-REM sleep ($t = -13.4$, $p < 0.01$), but still less in REM sleep ($t = 5.42$, $p < 0.01$). As a result, the time spent awake was not significantly different from the baseline night ($t = 0.84$, $p = 0.43$). During the final four-hour block of the night, magpies were awake less ($t = 4.07$, $p < 0.01$) and spent more time in non-REM sleep ($t = -4.73$, $p < 0.01$). REM sleep did not exceed baseline levels ($t = 1.15$, $p = 0.29$).

White light exposure also affected the duration and the number of bouts of each state (Table 5.2). During the four-hour block of light exposure, the duration of non-REM sleep bouts were shorter. During the second four-hour block (lights off), there were fewer but longer bouts of wakefulness, and bouts non-REM sleep were longer and less frequent, signalling that sleep was less fragmented during this period. In addition, bouts of REM sleep were shorter and less frequent during this block. During the final four-hour block of the night, there were fewer bouts of wakefulness, longer bouts of non-REM sleep and shorter bouts of REM sleep.

Recovery night – Exposure to white light also affected sleep recovery the following night (Table 5.1; Figure 5.2). During the first four-hour block of the recovery night, magpies spent slightly more time awake ($t = -3.99$, $p < 0.01$), and slightly less time in non-REM sleep ($t = 6.74$, $p < 0.01$), and REM sleep remained similar ($t = -1.58$, $p = 0.17$) as compared to same four-hour block of baseline night. During the next four-hour block, time spent awake (t = -1.49, p = 0.19) and in REM sleep (t = -1.43, p = 0.20) resembled baseline amounts, but magpies spent less time in non-REM sleep (t = 2.68, p = 0.04). Throughout the final four-hour block of the recovery night, magpie sleep composition resembled the equivalent four-hour block of the baseline night (Table 5.1).

Throughout the recovery night, bout length and episode number resembled that of the corresponding baseline night blocks with a few exceptions (Table 5.2). One, during the first four-hour block of the recovery night, bouts of non-REM sleep were shorter but more frequent. Two, during the second four-hour block of the recovery night, magpies had shorter bouts of non-REM sleep. Finally, during the last four-hour block non-REM sleep bouts were shorter and occurred more often.

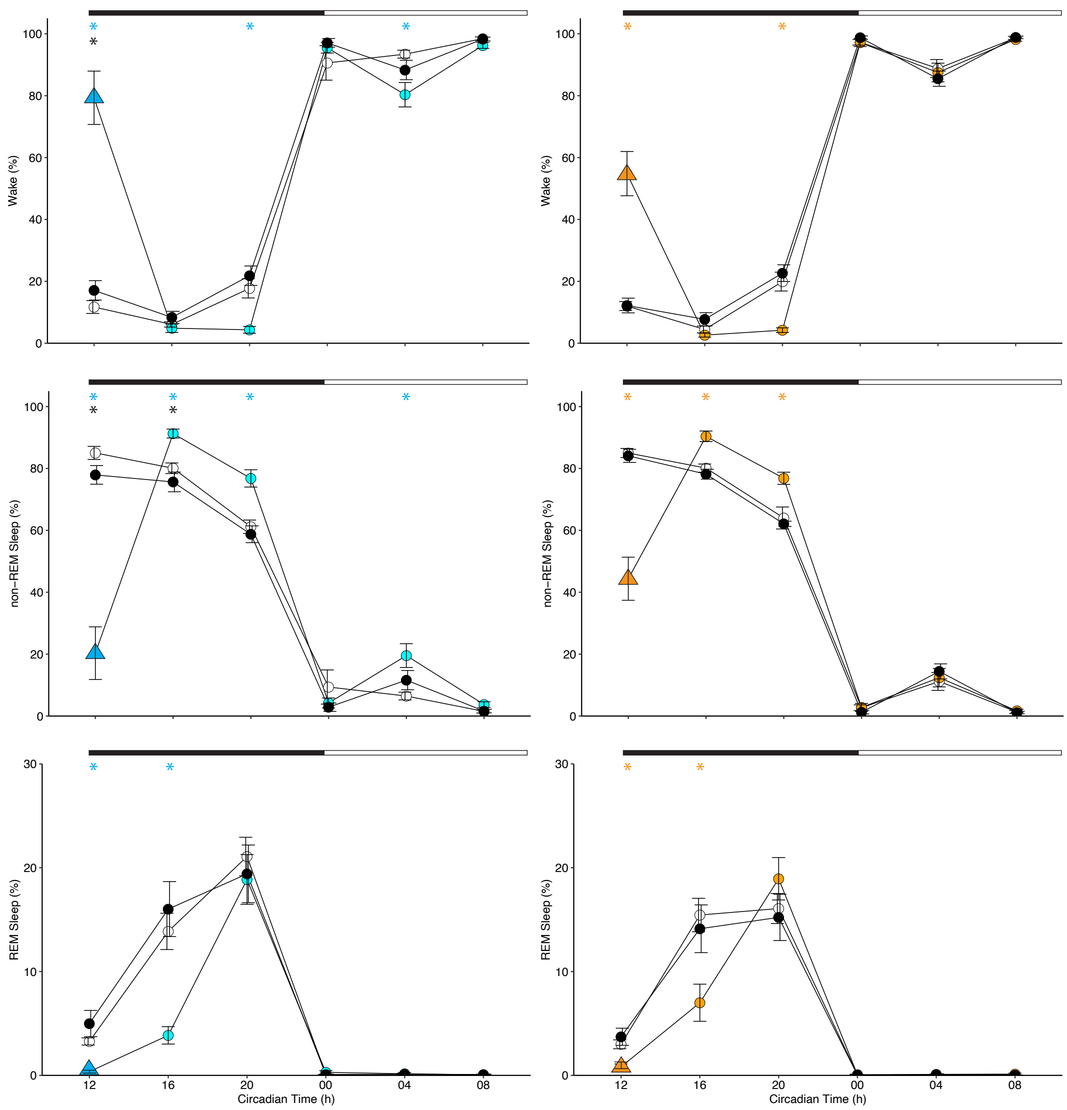


Figure 5.2. Effects of 4-h of white and amber light exposure on the percentage of wakefulness, non-REM and REM sleep. Data are summarised as 4-h time bins for the baseline (open), light treatment (blue: white light; orange: amber light), recovery (black). The 4-h of light exposure are represented by triangles (blue and orange). 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 quarter of the both light treatments night relative to baseline.

Table 5.1. Effects of white light on the mean night-time wakefulness (Wake), non-REM sleep (NREM), and REM sleep in magpies. Magpies (n = 7) were recorded during undisturbed 12-h (baseline night), followed by 4-h of white light exposure and an undisturbed 8-h (treatment night) and ending with 12-h of recovery (recovery night). Each night is separated into three 4-h blocks. Values are presented as mean ± SE along with p-values from paired t-tests that compared each quarter of the night (indicated by letters), paired by magpie identity.

Effects of white light on night time sleep and sleep recovery (4-h blocks)

	Baseline Night (B)			**Treatment Night (T)**			**Recovery Night (R)**		
	B1: 1200-1600	B2: 1600-2000	B3: 2000-0000	T1: 0000-0400	T2: 0400-0800	T3: 0800-1200	R1: 1200-1600	R2: 1600-2000	R3: 2000-2400
Wake	11.7 ± 2.1	6.1 ± 0.8	17.7 ± 3.1	79.3 ± 8.6	4.9 ± 1.4	4.3 ± 1.1	17.1 ± 3.1	8.3 ± 2.0	21.8 ± 3.1
NREM	85.0 ± 2.1	80.1 ± 1.7	61.2 ± 2.2	20.3 ± 8.5	91.3 ± 1.4	76.8 ± 2.8	77.9 ± 3.0	75.6 ± 3.2	58.7 ± 2.7
REM	3.3 ± 0.4	13.9 ± 1.7	21.1 ±1.9	0.4 ± 0.2	3.9 ± 0.8	18.9 ± 2.4	5.0 ± 1.3	16.0 ± 2.6	19.4 ± 2.8

	B1 – T1	B2 – T2	B3 – T3	B1 – R1	B2 – R2	B3 – R3
Wake	t = -9.44 **p < 0.01**	t = 0.84 p = 0.43	t = 4.07 **p < 0.01**	t = -3.99 **p < 0.01**	t = -1.49 p = 0.19	t = -1.59 p = 0.16
NREM	t = 9.42 **p < 0.01**	t = -13.4 **p < 0.01**	t = -4.73 **p < 0.01**	t = 6.74 **p < 0.01**	t = 2.68 **p = 0.04**	t = 1.08 p = 0.32
REM	t = 6.66 **p < 0.01**	t = 5.42 **p < 0.01**	t = 1.15 p = 0.29	t = -1.58 p = 0.17	t = -1.43 p = 0.20	t = 1.22 p = 0.27

Table 5.2. Effects of white light on the mean number and length of bouts of wakefulness (wake), non-REM sleep (NREM), and REM sleep in magpies during the night. Magpies (n = 7) were recorded during undisturbed 24-h (baseline), followed by 4-h of white light exposure and an undisturbed 20-h (treatment) and ending with 24-h of recovery (recovery). Each night is separated into three 4-h blocks. Values are presented as mean ± SE along with p-values from paired t-tests that compared each quarter of the night (indicated by letters), paired by magpie identity. REM sleep during the 4-h treatment was trivial and therefore excluded.

Effects of white light on night time sleep and sleep recovery (4-h blocks)

		Baseline Night (B)			Treatment Night (T)			Recovery Night (R)		
		B1: 1200-1600	B2: 1600-2000	B3: 2000-0000	T1: 1200-1600	T2: 1600-2000	T3: 2000-0000	R1: 1200-1600	R2: 1600-2000	R3: 2000-0000
Wake	no. bouts	57.4 ± 15.5	78.1 ± 16.4	89.6 ± 16.4	126.2 ± 34.7	23.1 ± 34.7	44.7 ± 10.6	75.3 ± 23.5	87.1 ± 23.3	142.4 ± 36.7
	bout length (s)	46.5 ± 13.5	12.5 ± 1.6	78.4 ± 40.0	67.7 ± 26.4	26.7 ± 5.7	16.2 ± 2.7	31.9 ± 6.8	16.4 ± 2.9	60.4 ± 16.4
NREM	no. bouts	123.3 ± 15.8	327.7 ± 17.7	421.9 ± 12.2	128.0 ± 33.6	111.9 ± 18.5	382.9 ± 27.6	168.3 ± 26.6	358.6 ± 16.0	451.3 ± 19.5
	bout length (s)	118.9 ± 19.9	34.2 ± 2.4	20.6 ± 0.6	26.4 ± 8.6	140.5 ± 22.6	29.8 ± 3.2	80.1 ± 13.9	30.6 ± 2.2	18.8 ± 1.0
REM	no. bouts	73.6 ± 0.7	263.1 ± 0.7	351.0 ± 0.5	-	89.4 ± 0.3	348.3 ± 0.6	101.6 ± 0.4	283.3 ± 0.8	333.0 ± 0.6
	bout length (s)	6.6 ± 0.7	7.5 ± 0.4	8.6 ± 0.5	-	6.0 ± 0.3	7.7 ± 0.6	6.8 ± 0.4	7.9 ± 0.8	8.2 ± 0.6

		B1 – T1	B2 – T2	B3 – T3	B1 – R1	B2 – R2	B3 – R3
Wake	no. bouts	t = -1.86 p = 0.12	t = 3.16 **p = 0.02**	t = 4.20 **p < 0.01**	t = -1.55 p = 0.17	t = -0.51 p = 0.63	t = -2.22 p = 0.07
	bout length (s)	t = -0.77 p = 0.48	t = -2.78 **p = 0.03**	t = 1.51 p = 0.18	t = 1.74 p = 0.13	t = -1.44 p = 0.20	t = 0.39 p = 0.71
NREM	no. bouts	t = -0.11 p = 0.92	t = 13.05 **p < 0.01**	t = 1.08 p = 0.32	t = -2.63 **p = 0.04**	t = -2.01 p = 0.09	t = -2.80 **p = 0.03**
	bout length (s)	t = 4.47 **p < 0.01**	t = -4.94 **p < 0.01**	t = -2.85 **p = 0.03**	t = 3.09 **p = 0.02**	t = 2.91 **p = 0.03**	t = 3.37 **p = 0.02**
REM	no. bouts	-	t = 7.24 **p < 0.01**	t = 0.08 p = 0.94	t = -1.79 p = 0.12	t = -0.99 p = 0.36	t = 1.01 p = 0.35
	bout length (s)	-	t = 3.90 **p < 0.01**	t = 2.90 **p = 0.03**	t = -0.31 p = 0.76	t = -1.00 p = 0.36	t = 1.13 p = 0.30

Baseline and post-treatment day – Exposure to white light for 4-h at night had a slight effect on subsequent daytime sleep (Figure 5.2). During the baseline day, the magpies spent 94.1 ± 1.8% of the day awake, 5.8 ± 1.8% in non-REM sleep, and 0.1 ± 0.0% in REM sleep. In comparison, during the day following the light treatment daytime sleep did not differ from the baseline day – wake: 90.7 ± 1.8% ($t = -1.55$, $p = 0.17$); non-REM sleep: 9.2 ± 1.7% ($t = 1.51$, $p = 0.18$); REM: 0.2 ± 0.1% ($t = -1.48$, $p = 0.19$). However, birds did show an increase in non-REM sleep ($t = 3.74$, $p < 0.01$) during the middle 4-h of the day (0400 h – 0800 h circadian time). Additionally, bouts of wakefulness were shorter and there were more bouts of non-REM sleep during the post-treatment day (Table 5.3).

Recovery day – Magpies did not show any significant differences in sleep composition during the recovery day compared to the baseline day – wake: 94.6 ± 1.4 ($t = -0.25$, $p = 0.81$); non-REM sleep: 5.4 ± 1.3% ($t = 0.26$, $p = 0.80$); REM sleep: 0.1 ± 0.0% ($t = -0.17$, $p = 0.87$). Similarly, there were no differences in bout length or frequency (Table 5.3).

Table 5.3. Effects of white light on the mean number and length of bouts of wakefulness (wake) and non-REM sleep (NREM) in magpies during the day. Magpies (n = 7) were recorded during undisturbed 24-h (baseline), followed by 4-h of white light exposure and an undisturbed 20-h (treatment) and ending with 24-h of recovery (recovery). Each day is represented by a 12-h blocks Values are presented as mean ± SE along with p-values from paired t-tests that compared each quarter of the night (indicated by letters), paired by magpie identity. REM sleep during the daytime was trivial and therefore excluded.

Effects of white light on daytime sleep and sleep recovery (12-h block)

		Day 1 Baseline (B)	Day 2 Treatment (T)	Day 3 Recovery (R)	B – T	T – R	B – R
Wake	no. bouts	246.6 ± 49.5	331.3 ± 42.7	259.4 ± 62.7	t = -2.29 p = 0.06	t = 2.32 p = 0.06	t = -0.29 p = 0.79
	bout length (s)	249.4 ± 67.9	143.5 ± 30.6	749.3 ± 607.7	t = -2.70 **p = 0.04**	t = -1.04 p = 0.34	t = -0.91 p = 0.40
NREM	no. bouts	247.0 ± 50.3	341.1 ± 44.9	261.3 ± 64.2	t = -2.64 **p = 0.04**	t = 2.64 **p = 0.04**	t = -0.30 p = 0.78
	bout length (s)	10.0 ± 1.3	11.7 ± 1.7	8.5 ± 1.1	t = -1.05 p = 0.33	t = 1.69 p = 0.14	t = 1.14 p = 0.30

Slow wave activity at night – During the baseline night, mean SWA declined ($F_{2,18}$ = 72.1, $p < 0.01$) and was highest during the first third of the night (Figure 5.2). In contrast, mean SWA increased across the night after exposure to four hours of white light ($F_{2,17}$ = 3.6, $p = 0.05$). During the first four-hour block of the treatment night, SWA was the lowest (93.5 ± 10.3%; t = 2.51, p = 0.05) relative to the same baseline night block (121.8 ± 2.5%). During the second four-hour block, SWA was higher during the treatment night (119.5 ± 10.1%; t = -3.07, p = 0.02) relative to the equivalent baseline night block (89.4 ± 1.8%). During the final four-hour block, treatment night SWA (88.7 ± 6.0%; t = -1.31; p = 0.24) and baseline night SWA (83.3 ± 2.9%) were comparable. SWA decreased throughout the recovery night ($F_{2,18}$ = 10.0, $p < 0.01$). During the recovery night, SWA was lower (78.7 ± 3.8%; t = 4.3, p < 0.01) compared to the baseline night.

Slow wave activity during the 12-h day – During the baseline day, mean SWA did not vary with time of day ($F_{2,14}$ = 4.4, $p = 0.14$) but was highest at the beginning of the day (Figure 5.3). Mean SWA did not vary throughout the treatment day ($F_{2,18}$ = 2.6, $p = 0.10$). There was no significant change in daytime SWA across the recovery day ($F_{2,16}$ = 2.03, $p = 0.16$).

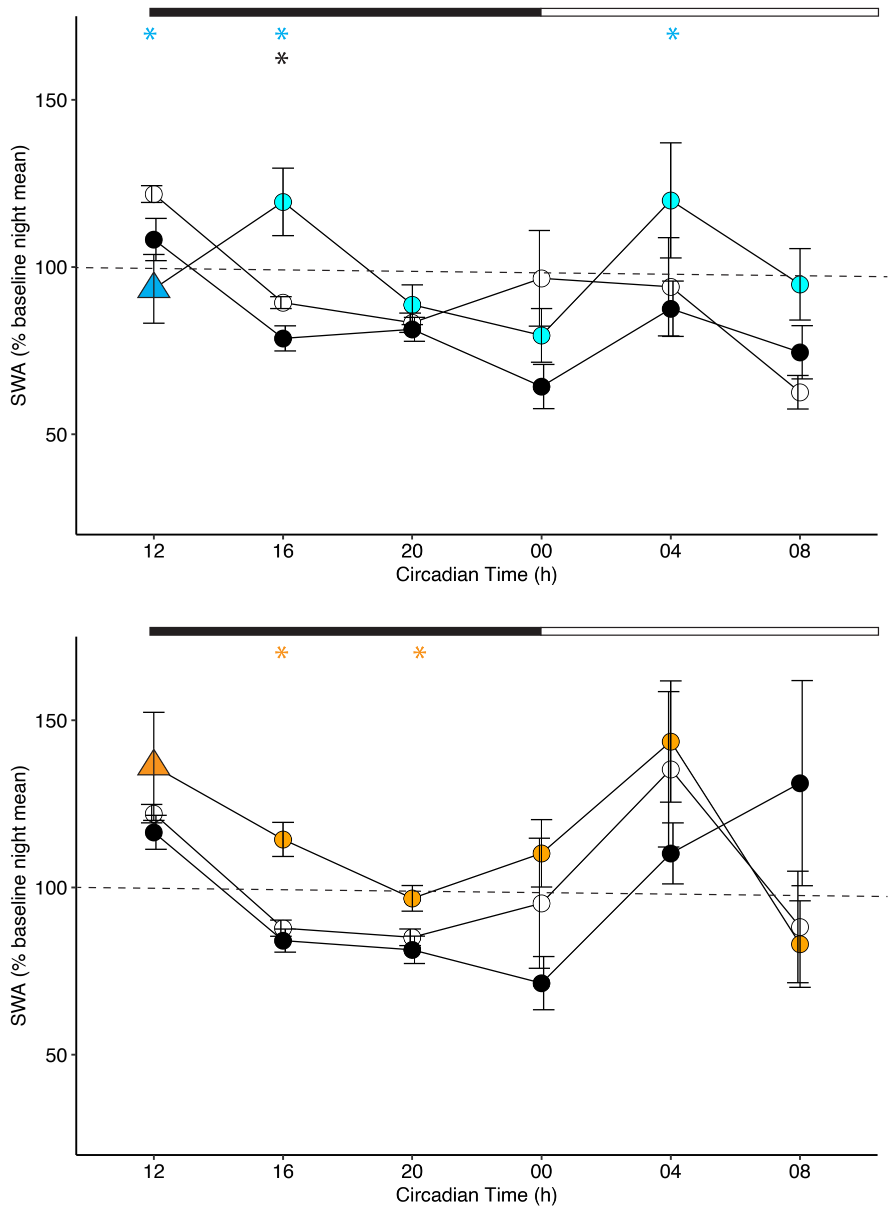


Figure 5.3. Effects of 4-h of white and amber light exposure on non-REM sleep-related slow wave activity (SWA; 0.78 – 3.91 Hz power density). Data are summarised as 4-h time bins for the baseline (open), light treatment (blue: white light; orange: amber light), recovery (black). The 4-h of light exposure are represented by triangles (blue and orange). SWA is expressed as a percentage of the baseline night non-REM sleep mean (i.e. the 100% dashed line). Circadian time plots lights on/off at 0/12 h, respectively; the horizontal bar along the top of the figure indicates photoperiod. 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 higher during the second quarter of both light treatment nights relative to baseline.

(II) Effects of amber light on sleep and sleep recovery

Baseline and treatment night – In the first four-hour block of the baseline night, magpies spent 12.0 ± 1.4% of the time awake, 85.0 ± 1.5% in non-REM sleep, and 3.0 ± 0.4% in REM sleep (Table 5.4; Figure 5.2). During the second four-hour block of the baseline night, magpies spent 4.4 ± 1.1% of the time awake, 80.1 ± 1.3% in non-REM sleep, and 15.4 ± 1.6% in REM sleep. During the final four-hour block of the baseline night, magpies spent 19.9 ± 3.0% of the time awake, 64.0 ± 3.6% in non-REM sleep, and 16.1 ± 1.4% in REM sleep.

The following night, birds were exposed to four hours of amber light (Table 5.4; Figure 5.2). During the four-hour block of amber light exposure, time spent awake increased ($t = -5.74$, $p < 0.01$), non-REM sleep decreased ($t = 5.44$, $p < 0.01$) and REM sleep decreased ($t = 7.46$, $p < 0.01$) compared to the same four-hour block of the baseline night. After four hours, lights were turned off and birds had eight hours of darkness before lights on at 0600 h. During the first four-hour block of darkness following light exposure (temporally matched to the second four-hour block of the baseline night), the time magpies spent awake ($t = 1.57$, $p = 0.17$) did not differ significantly from the baseline night, but they spent more time in non-REM sleep ($t = -7.75$, $p < 0.01$) and less time in REM sleep ($t = 8.94$, $p < 0.01$). During the next four-hour block of darkness, magpies were awake less ($t = 4.61$, $p < 0.01$), and spent more time in non-REM sleep ($t = -5.70$, $p < 0.01$). REM sleep did not differ significantly from the corresponding baseline block.

Amber light exposure also affected the duration and the total number of bouts of each episode (Table 5.5). During the four-hour block of light exposure, there were more bouts of both wakefulness. During the second four-hour block (amber light turned off), there were fewer bouts of non-REM sleep and REM sleep. During the final four-hour block of the night, bouts of non-REM sleep were longer and there were fewer bouts of wakefulness. There were no striking differences in REM sleep between the baseline and treatment night during this four-hour block.

Recovery night – The four-hour exposure to amber light had no effect on sleep amount or composition during the recovery night (Table 5.4; Figure 5.2). During each four-hour block, magpie sleep resembled that of the corresponding four-hour blocks of the baseline night with two exceptions. One, during the first four-block of the night, bouts of wakefulness were significantly shorter (Table 5.5). Two, during the final four hours of the night there were more bouts non-REM sleep.

Table 5.4. Effects of amber light on the mean night-time wakefulness (Wake), non-REM sleep (NREM), and REM sleep in magpies. Magpies (n = 7) were recorded during undisturbed 12-h (baseline night), followed by 4-h of amber light exposure and an undisturbed 8-h (treatment night) and ending with 12-h of recovery (recovery night). Each night is separated into three 4-h blocks. Values are presented as mean ± SE along with p-values from paired t-tests that compared each quarter of the night (indicated by letters), paired by magpie identity.

Effects of amber light on night time sleep and sleep recovery (4-h blocks)

	Baseline Night (B)			**Treatment Night (T)**			**Recovery Night (R)**		
	B1: 1800-2200	B2: 2200-0200	B3: 0200-0600	T1: 1800-2200	T2: 2200-0200	T3: 0200–0600	R1: 1800-2200	R2: 2200-0200	R3: 0200-0600
Wake	12.0 ± 1.4	4.4 ± 1.1	19.9 ± 3.0	54.8 ± 7.1	2.6 ± 0.6	4.2 ± 0.8	12.2 ± 2.3	7.7 ± 2.2	22.7 ± 2.7
NREM	85.0 ± 1.5	80.1 ± 1.3	64.0 ± 3.6	44.4 ± 7.0	90.4 ± 1.7	76.8 ± 2.0	84.1 ± 2.1	78.2 ± 1.6	62.1 ± 0.8
REM	3.0 ± 0.4	15.4 ± 1.6	16.1 ± 1.4	0.8 ± 0.3	7.0 ± 1.8	18.9 ± 2.0	3.7 ± 0.8	14.1 ± 2.3	15.2 ± 2.2

	B1 – T1	B2 – T2	B3 – T3	B1 – R1	B2 – R2	B3 – R3
Wake	t = -5.74 **p < 0.01**	t = 1.57 p = 0.17	t = 4.61 **p < 0.01**	t = -0.07 p = 0.95	t = -1.57 p = 0.17	t = -1.09 p = 0.32
NREM	t = 5.44 **p < 0.01**	t = -7.75 **p < 0.01**	t = -5.70 **p < 0.01**	t = 0.38 p = 0.71	t = 1.72 p = 0.13	t = 0.59 p = 0.58
REM	t = 7.46 **p < 0.01**	t = 8.94 **p < 0.01**	t = -1.74 p = 0.13	t = -0.82 p = 0.44	t = 0.54 p = 0.61	t = 0.32 p = 0.76

Table 5.5. Effects of amber light on the mean number and length of bouts of wakefulness (Wake), non-REM sleep (NREM), and REM sleep in magpies at night. Magpies (n = 7) were recorded during undisturbed 24-h (baseline), followed by 4-h of amber light exposure and an undisturbed 20-h (treatment) and ending with 24-h of recovery (recovery). Each night is separated into three 4-h blocks. Values are presented as mean ± SE along with p-values from paired t-tests that compared each quarter of the night (indicated by letters), paired by magpie identity. REM sleep during the 4-h treatment was trivial and therefore excluded.

Effects of amber light on night time sleep and sleep recovery (4-h blocks)

		Baseline Night (B)			**Treatment Night (T)**			**Recovery Night (R)**		
		B1: 1200-1600	B2: 1600-2000	B3: 2000-0000	T1: 0000-0400	T2: 0400-0800	T3: 0800-1200	R1: 1200-1600	R2: 1600-2000	R3: 2000-2400
Wake	no. bouts	46.0 ± 12.8	41.0 ± 15.6	131.0 ± 24.3	107.4 ± 30.2	22.1 ± 2.2	47.9 ± 8.7	65.7 ± 17.4	85.9 ± 22.1	198.0 ± 42.9
	bout length (s)	50.2 ± 8.6	19.9 ± 3.2	59.9 ± 18.9	51.7 ± 8.7	14.6 ± 0.9	15.1 ± 2.9	22.5 ± 3.1	14.0 ± 2.1	38.6 ± 7.8
NREM	no. bouts	109.1 ± 15.7	321.6 ± 21.3	413.1 ± 21.6	121.0 ± 29.6	152.7 ± 22.6	386.4 ± 26.7	136.7 ± 17.0	33.9 ± 14.3	471.1 ± 22.8
	bout length (s)	133.1 ± 26.3	36.9 ± 2.6	22.9 ± 2.3	85.0 ± 22.3	106.8 ± 33.2	29.7 ± 3.4	102.7 ± 17.7	33.0 ± 1.4	19.1 ± 0.7
REM	no. bouts	68.0 ± 0.5	286.9 ± 0.6	295.6 ± 0.7	-	134.3 ± 1.1	346.7 ± 0.7	77.7 ± 0.6	257.1 ± 0.5	297.6 ± 0.3
	bout length (s)	6.3 ± 0.5	7.7 ± 0.6	7.8 ± 0.7	-	7.0 ± 1.1	7.8 ± 0.7	6.4 ± 0.6	7.7 ± 0.5	7.3 ± 0.3

		B1 – T1	B2 – T2	B3 – T3	B1 – R1	B2 – R2	B3 – R3
Wake	no. bouts	t = -3.32 **p = 0.02**	t = 1.27 p = 0.25	t = 3.19 **p = 0.02**	t = -1.37 p = 0.22	t = -2.06 p = 0.09	t = -2.32 p = 0.06
	bout length (s)	t = -0.25 p = 0.81	t = 1.87 p =0.11	t = 2.25 p =0.07	t = 3.49 **p = 0.01**	t = 2.04 p = 0.09	t = 1.11 p = 0.31
NREM	no. bouts	t = -0.64 p =0.54	t = 5.57 p < 0.01	t = 2.27 p = 0.06	t = -1.98 p = 0.10	t = -0.53 p = 0.62	t = -2.79 p = 0.03
	bout length (s)	t = 2.00 p = 0.09	t = -2.19 p = 0.07	t = -4.82 **p < 0.01**	t = 1.05 p = 0.34	t = 1.23 p = 0.27	t = 1.76 p = 0.13
REM	no. bouts	-	t = 6.65 **p < 0.01**	t = -1.83 p = 0.12	t = -0.56 p = 0.60	t = 0.69 p = 0.51	t = -0.05 p = 0.97
	bout length (s)	-	t = 1.56 p = 0.17	t = 0.16 p = 0.88	t = -0.38 p = 0.72	t = 0.17 p = 0.87	t = 1.07 p = 0.32

Baseline and Treatment Day – During the amber baseline day, magpies spent 94.9 ± 0.9% of the day awake, 5.1 ± 0.9% in non-REM sleep, and 0.00 ± 0.0% in REM sleep (Figure 5.2). The post-treatment day showed no difference in the time spent awake (94.3 ± 1.3%; $t = 0.95$, $p = 0.38$) in non-REM sleep (5.6 ± 1.3%; $t = -0.88$, $p = 0.41$), or in REM sleep (0.1 ± 0.0%; $t = -2.04$, $p = 0.09$). During the post-treatment day, bout duration and number of episodes did not differ significantly from the baseline day (Table 5.6).

Recovery day – During the amber recovery day, the time spent awake (94.4 ± 0.8%; $t = 1.78$, $p = 0.13$), in non-REM sleep (5.6 ± 0.8%; $t = -1.78$, $p = 0.13$) and in REM sleep resembled baseline day amounts (0.0 ± 0.0%; $t = 0.16$, $p = 0.88$; Figure 5.2). Bout duration and number of episodes did not differ significantly from the baseline day (Table 5.6).

Table 5.6. Effects of amber light on the mean number and length of bouts of wakefulness (Wake) and non-REM sleep (NREM) in magpies during the day. Magpies (n = 7) were recorded during undisturbed 24-h (baseline), followed by 4-h of amber light exposure and an undisturbed 20-h (treatment), and ending with 24-h of recovery (recovery). Each day is represented by 12-h blocks. Values are presented as mean ± SE along with p-values from paired t-tests that compared each quarter of the night (indicated by letters), paired by magpie identity. REM sleep during the daytime was trivial and therefore excluded.

Effects of amber light on daytime sleep and sleep recovery (12-h block)

		Day 1 Baseline	Day 2 Treatment	Day 3 Recovery	B – T	T – R	B – R
Wake	no. bouts	221.9 ± 46.9	229.3 ± 49.3	268.9 ± 43.2	t = -0.33 p = 0.75	t = -2.32 p = 0.06	t = -2.00 p = 0.09
	bout length (s)	316.1 ± 151.5	305.9 ± 125.4	191.0 ± 60.8	t = 0.28 p = 0.79	t = 1.72 p = 0.14	t = 1.37 p = 0.22
NREM	no. bouts	220.6 ± 46.8	228.4 ± 49.6	267.4 ± 42.6	t = -0.34 p = 0.75	t = -1.15 p = 0.30	t = -2.01 p = 0.09
	bout length (s)	10.6 ± 1.7	10.8 ± 1.2	10.3 ± 1.6	t = -0.16 p = 0.88	t = 0.45 p = 0.67	t = 0.16 p = 0.88

Slow wave activity at night – During the baseline night, mean SWA decreased with time of night ($F_{2,18} = 65$, $p < 0.01$) and was highest during the first half of the night (Figure 5.3). Similar to the baseline night, mean SWA during exposure to amber light was highest in the beginning of the night and subtly decreased throughout the night ($F_{2,18} = 3.89$, $p = 0.04$). Interestingly, unlike white light, during the first four-hour block of amber light exposure, SWA (136.2 ± 16.2%) was not different relative to baseline (122.1 ± 2.8%; t = -0.98, p = 0.37). During the second and third four-hour block (with experimental lights turned off), SWA was higher on the treatment night (second: 113.8 ± 4.8%; t = -3.75, p < 0.01; third: 96.7 ± 3.8%; t = -3.59, p = 0.01) relative to the baseline (second: 87.8 ± 2.4%; third: 85.1 ± 2.5%). On the recovery night, SWA was highest at the start and declined throughout the night ($F_{2,18} = 21$, $p < 0.01$). There was no significant difference in SWA between the baseline night and the recovery night.

Slow wave activity during the day – During the baseline day, mean SWA did not vary significantly with time of day ($F_{2,15} = 1.54$, $p = 0.25$) (Figure 5.2). During the post-treatment day, mean SWA was higher compared to the baseline day ($F_{2,14} = 3.99$, $p = 0.04$). SWA increased throughout the recovery day ($F_{2,15} = 2.26$, $p = 0.14$). There was no significant difference in SWA between the baseline day and the recovery day.

(III) Differences between white and amber light exposure

Baseline night and day – The baseline sleep composition (night and day) prior to the both light treatments were not statistically different (Table 5.1; Table 5.4). – baseline night: wake ($t = -0.24$, $p = 0.82$), non-REM sleep ($t = -0.96$, $p = 0.38$), REM sleep ($t = 1.20$, $p = 0.29$); baseline day: wake ($t = -0.82$, $p = 0.45$), non-REM sleep ($t = 0.08$, $p = 0.46$), and REM sleep ($t = 1.07$, $p = 0.34$).

Treatment night – Sleep composition differed significantly depending on the colour of the light exposure. During the four-hour light exposure birds were awake more ($t = 4.08$, $p < 0.01$) and spent less time in non-REM sleep ($t = -4.09$, $p = 0.01$) in white light (Table 5.1; Figure 5.2) as compared to amber (Table 5.4). Throughout the entire 12-hour night, magpies exposed to white light were awake more (white: 29.5 ± 3.0%; amber: 20.6 ± 2.4%; $t = 4.29$, $p < 0.01$) and spent less time in non-REM sleep (62.8 ± 3.2%) than did magpies exposed to amber light (70.5 ± 1.9%; $t = -3.13$, $p = 0.03$). REM sleep was unaffected by light wavelength (white: 7.7 ± 1.0%; amber: 8.9 ± 1.3%; $t = 0.15$, $p = 0.88$).

I found no significant differences in mean bout length or mean number of bouts of wakefulness, non-REM sleep, or REM sleep between the white and amber light treatment nights.

Post-treatment day – The two light colours did not differ in their impact on sleep composition throughout the day following exposure (Figure 5.2). Throughout the 12-hour day, time spent awake, in non-REM sleep, and in REM sleep were similar in both light treatments (wake – white: 90.7 ± 1.8%; amber - 94.3 ± 1.3%; $t = -2.3$, $p = 0.07$; non-REM – white: 9.16 ± 1.7%; amber – 5.6 ± 1.3%; $t = 2.18$, $p = 0.08$; REM – white: 0.2 ± 0.1%; amber – 0.1 ± 0.0%; $t = 0.91$, $p = 0.41$). I found no significant differences in mean bout length or mean number of bouts of wakefulness or non-REM sleep between the white and amber light post treatment days.

Recovery night – The colour of exposed light also had an impact on the recovery night. During the first four hours of the recovery night birds that had been exposed to white light were awake more ($t = 4.2$, $p < 0.01$) and spent less time in non-REM sleep ($t = -4.09$, $p < 0.01$) compared to birds exposed to amber light (Figure 5.2). No other differences were seen throughout the recovery night.

Slow wave activity – There were no differences between the two light treatment colours on SWA throughout the treatment night, post-treatment day, or recovery night.

(IV) Order Effect: effect of treatment order

The order in which light treatments were presented (white first or amber first) did have an effect on some aspects of sleep composition; however, these effects were not seen during the baseline day and therefore would have most likely reflected different effects of the light treatments on individual birds and not the order of exposure (Table 5.7).

Table 5.7. Effects of light treatment order on the mean wakefulness (Wake), non-REM sleep (NREM), and REM sleep in magpies. This table shows p-values from paired t-tests comparing means across all nights and days and the order of exposure of white and amber light for each light experiment (white and amber).

Order effect on sleep and sleep recovery (12-hour bin)						
	White Light Exposure *white treatment first vs amber treatment first*			**Amber Light Exposure** *amber treatment first vs white treatment first*		
	Night 1 Baseline	Night 2 Treatment	Night 3 Recovery	Night 1 Baseline	Night 2 Treatment	Night 3 Recovery
Wake	t = 0.27 p = 0.80	t = -0.88 p = 0.46	t = -0.13 p = 0.90	t = -1.43 p = 0.24	t = -0.72 p = 0.50	t = -1.93 p = 0.17
NREM	t = -0.12 p = 0.91	t = 0.32 p = 0.78	t = -0.38 p = 0.73	t = 1.57 p = 0.18	t = 0.92 p = 0.40	t = 2.08 p = 0.09
REM	t = 0.43 p = 0.70	t = 2.94 p = **0.03**	t = 0.51 p = 0.66	t = -0.70 p = 0.53	t = 3.95 p = 0.98	t = 0.98 p = 0.38
	Day 1 Baseline	Day 2 Treatment	Day 3 Recovery	Day 1 Baseline	Day 2 Treatment	Day 3 Recovery
Wake	t = -2.0 p = 0.20	t = -0.30 p = 0.80	t = -1.0 p = 0.4	t = -3.0 p = 0.09	t = -4.0 p **= 0.01**	t = -3.0 **p = 0.05**
NREM	t = 2.0 p = 0.20	t = 0.30 p = 0.80	t = 1.0 p = 0.4	t = 3.0 p = 0.09	t = 4.0 p **= 0.01**	t = 3.0 **p = 0.04**
REM	t = 0.80 p = 0.50	t = 0.30 p = 0.80	t = -0.09 p = 0.90	t = 1.0 p = 0.30	t = 2.0 p = 0.20	t = 0.70 p = 0.50

5.5 | Discussion

Australian magpies exposed to four hours of ecologically relevant light intensities of two different colours (white and amber) during the night slept less and had more fragmented sleep. After lights were turned off, the non-REM sleep lost during light exposure was recovered by engaging in more non-REM sleep and by increasing non-REM sleep intensity (measured as SWA). However, no evidence for REM sleep homeostasis was seen, with magpies showing no REM sleep recovery. Finally, I found that white, blue-rich lighting had a more disruptive impact on sleep than amber, blue-reduced lighting. These findings provide experimental evidence that part-night exposure to an ecologically relevant lighting disrupts sleep electrophysiology in birds, the impacts of which persist throughout the remainder of the night. Furthermore, these results show that white, blue-rich lighting disrupts sleep more than amber, blue-reduced lighting.

During the four hours of exposure to white and amber light, birds spent more time awake and less time in non-REM and REM sleep compared to an equivalent dark period. White light had a greater effect on sleep than did amber light; birds exposed to white light were awake for an hour more than when exposed to amber light (3.5 h and 2.5 h respectively). The four-hour exposure to white light also had an impact on sleep intensity, which is illustrated by the reduction of SWA during non-REM sleep. In contrast, birds exposed to amber light showed marginally higher sleep intensity, indicating that birds were not only able to sleep more during amber light exposure compared to white light exposure, but that sleep intensity during amber light also resembled baseline sleep. Overall, compared to a dark night, birds exposed to white light lost two hours of sleep, while birds exposed to amber light lost only one hour, providing further evidence that blue-rich lighting may have a greater impact on sleep than blue-reduced lighting.

Light also affected sleep composition following exposure. In the eight hours following light exposure, birds spent less time awake, more time in non-REM sleep and showed increased non-REM sleep intensity compared to the same eight-hour time period on the baseline night. This suggests that the magpies increased sleep duration and intensity to make up for lost sleep following exposures to both light regimes. This is consistent with studies on mammals and birds, showing that animals can compensate for reductions in sleep by increasing SWA during sleep (Lesku et al., 2011a; Martinez-Gonzalez et al., 2008). Comparing the two light colours, white light had a greater impact on sleep than did amber light. Overall, throughout the entire the treatment night, birds exposed to white light experienced a greater amount of sleep disturbance compared to amber light. This result was expected and similar to the results of studies on humans (Ayaki et al., 2016; Santhi et al., 2012; Van Der Lely et al., 2015).

Light exposure had only a marginal effect on daytime sleep in both treatments. There were no differences between daytime sleep following either white or amber light exposure compared to the baseline day. However, birds spent less time awake in the middle part of the day (0400 h – 0800 h circadian time) following the white light exposure. This spike in sleep during the middle four hours of the day was not seen following amber light exposure, suggesting magpies may have slept more following white light exposure. These results provide further evidence of greater negative impacts associated with white light exposure compared to amber light exposure.

Magpies did not experience any rebound in REM sleep. During the light exposure nights, magpies lost a total of 36 minutes and 19 minutes of REM sleep in white and amber light respectively. During the recovery night, however, birds only recovered six minutes of lost REM sleep following the white treatment and failed to recover any of the lost REM sleep following the amber treatment. This absence of a robust REM sleep rebound is inconsistent with prior research, which suggests that the amount of REM sleep should increase following sleep disruption to maintain REM sleep homeostasis (Martinez-Gonzalez et al., 2008; Tisdale et al., 2018; Tobler & Borbély, 1988). Absence of REM sleep rebound in magpies was similarly seen in my previous study of sleep in magpies (*Chapter 4*) and has also been reported in starlings (*Sturnus vulgaris;* van Hasselt et al., 2019), further throwing into question the necessity of a REM sleep rebound following REM sleep loss. There are two possible explanations for this result. First, magpies do not show a robust REM sleep rebound following sleep loss; and second, the REM sleep loss generated by these two light exposures was too small to warrant a significant rebound. A study looking at complete sleep deprivation in birds may provide more insight into the REM sleep rebounds in magpies.

While this study aligns with previous studies in humans and animals, it is also important to acknowledge its potential limitations. First, despite the light intensity reflecting what is found in urban areas, wildlife may be able to avoid brightly lit areas completely by simply changing their sleeping location to a less illuminated area (Dominoni et al., 2014; Yorzinski et al., 2015), unlike the magpies in this study, which were unable to avoid the light exposure. Second, I did not to collect blood and was unable to determine the effect different coloured lights had on circulating melatonin. Still, by exposing birds to light for only part of the night, I found that both white and amber light appear to have caused a visual disturbance, disrupting sleep primarily during light exposure and not once lights were turned off. In addition, white light had a longer-term presumably physiological effect which is seen during the post-treatment day and recovery night.

Ultimately, these results demonstrate that light at night, even for just a few hours, can have severe impacts on sleep, which continue throughout the next day and night; and, that blue-rich lighting can be more harmful for night-time sleep in birds than blue-reduced lighting. While my findings about blue-rich lighting reflects results found in humans (Ayaki et al., 2016; Santhi et al., 2012; Van Der Lely et al., 2015), it contradicts a study in mice that shows no difference between blue-rich and blue-reduced lighting on sleep (Mouland et al., 2019). These contrasting impacts of blue-rich lighting on humans and magpies, and on mice, emphasize the fallacy in applying a result found in a single species to all taxa. Differences in sleep are seen even between closely related species (Libourel et al., 2018). It is therefore imperative we study sleep across a richer diversity of species to better understand how artificial light at night and other anthropogenic changes impact wildlife. Poor sleep can have lasting effects on health, survival and reproductive success in wildlife and therefore, there is a pressing need for further research to better offer mitigation strategies to protect both animals and humans alike.

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Chapter 6 – Conclusions and future directions

Photograph: Male and female Australian magpie duet (Photo by Dr. Michelle Hall)

6.1 | General Discussion

This thesis explores the impact of two anthropogenic pollutants (urban noise and artificial light at night) on two vital biological processes (cognitive function and sleep) in a city-dwelling passerine, the Australian magpie (*Cracticus tibicen tyrannica*).

The key findings (summarised in Figure 6.1) are that higher amplitudes of anthropogenic noise have little or no apparent effect on cognitive performance in wild birds, either in their natural environment (*Chapter 2*) or in captivity (*Chapter 3*), and that urban noise does not have a strong or pervasive impact on cognitive development (*Chapter 2*). In addition, my research provides evidence that anthropogenic noise (*Chapter 4*) and artificial light at night (*Chapter 5*) reduce the overall duration of sleep and alter its composition and intensity; and that blue-enriched lighting had a greater impact on sleep than blue-reduced lighting (*Chapter 5*). Finally, I found no evidence for the recovery of lost REM sleep (*Chapter 4* and *5)*, challenging the widespread perception that this sleep state has an essential, restorative function.

Below, I review the main results and their broader implications, and suggest avenues for future research.

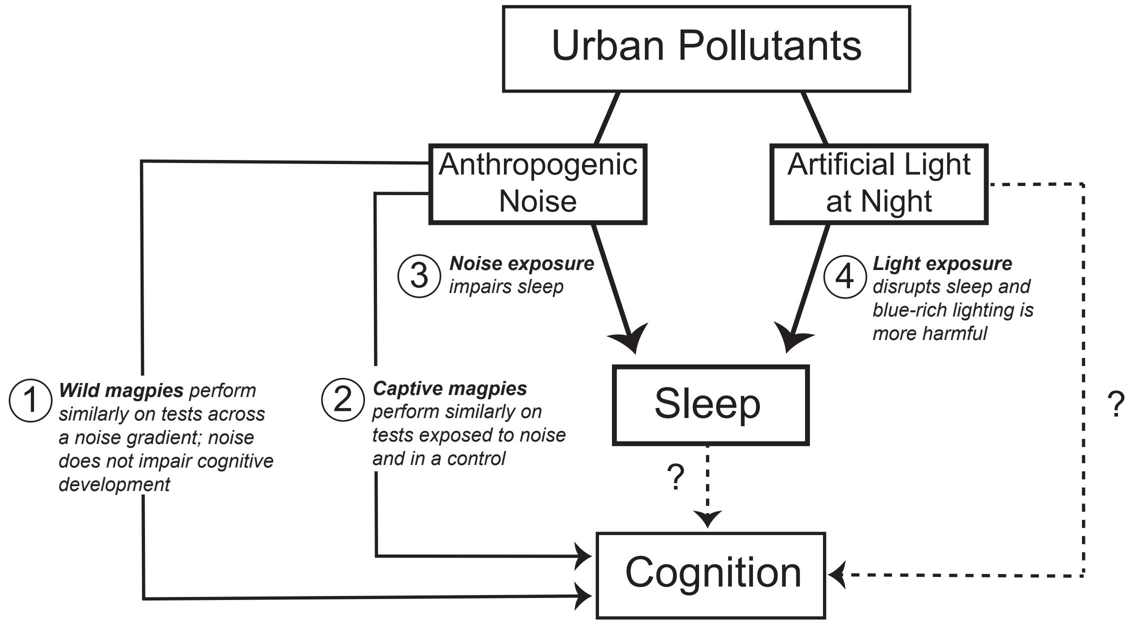

Figure 6.1: Summary of hypothesised pathways (numbered solid lines (1 – 4) each correspond to a thesis chapter) linking urban pollutants to sleep and cognition which are explored in this thesis. Pathways marked with dotted lines and (?) indicate hypothesised pathways that remain unexplored.

6.2 | Anthropogenic Noise and Cognition

To my knowledge, this study is the first to investigate the effect of anthropogenic noise on cognitive performance in a wild bird across both natural and captive contexts. Wild Australian magpies occupying habitats across an urban noise gradient showed no reduction in cognitive performance when exposed to higher levels of environmental noise (*Chapter* 2). In the wild, age was the strongest indicator of performance and adults performed better than subadults across a suite of cognitive tests. This result is perhaps unsurprising, as similar improvements with age have been demonstrated on cognitive tasks in other species (e.g. Bugnyar et al., 2007). In addition, I found that changes in the cognitive performance of wild juveniles at two different life stages were affected by the level of environmental noise to which they were exposed, but in only one of four cognitive tests (spatial memory; *Chapter 2*). The detrimental effect of noise on spatial memory matches findings in rats (Barzegar et al., 2015; Hu et al., 2014), while the lack of any observable effect on noise on the development of other cognitive tasks contradicts findings in mice (Jafari et al., 2018).

In captivity, magpies showed no difference in cognitive performance when exposed to either noisy or quiet (control) conditions (Chapter 3). Prior experience with a given cognitive task had the greatest impact on performance, with birds performing better on the task the second time they attempted it (*Chapter 3*). As described in *Chapter 3*, birds performed well on discrimination and learning tasks, so improvement on a second trial was not unexpected. However, the results of these experiments contradicted my expectation that higher noise levels would impair cognitive performance and development.

My findings are somewhat challenging to reconcile with those from other studies reporting negative impacts of noise on a range of biological functions (Dominoni et al., 2016; Funabiki & Konishi, 2003; Kleist et al., 2018; Potvin, 2017) and also, my experimental findings that noise can disrupt sleep (described below; *Chapter* 4), which is known to be important to cognitive functioning (Derégnaucourt et al., 2005; Huber et al., 2004; Tononi & Cirelli, 2016; Van Dongen et al., 2003).

Assuming my findings are both robust and general, they could be explained by the fact that birds in urban environments often possess behavioural traits (including increased innovation) which allow them to thrive in the complex environments that characterise cities, irrespective of negative factors associated with urban living (Griffin et al., 2017a; Sol et al., 2012). The subjects in this study were all residents of suburbs of a large metropolitan city and were presumably descended from generations of magpies that occupied similar habitats. Hence, they may either be highly tolerant of (desensitised to) noise, and/or have evolved adaptions to counter the potentially negative impacts of anthropogenic noise. This possibility could be evaluated by repeating the captive experiment from *Chapter 3* with magpies naïve to urban noise (e.g. from rural areas). If the cognitive performance of rural magpies is similarly unimpacted by anthropogenic noise, this would suggest that no compensatory adaptations are necessary, and that magpies essentially possess a set of traits that 'pre-adapt' them for urban living (Palacio, 2020; Potvin, 2017; Sol et al., 2012). While urban-rural comparisons are common in a range of studies exploring anthropogenic impacts (Audet et al., 2016; Federspiel et al., 2017; Preiszner et al., 2016), no study has yet succeeded in isolating the effects of anthropogenic noise from other potentially correlated confounds.

My finding that noise does not impact cognition hinges on the assumption that the tests I used to analyse cognitive function were ecologically relevant to magpies. This is likely for two reasons. First, I used a suite of tests that were previously validated in Western Australia, and tested several cognitive pathways

(Ashton et al., 2018). Second, each test was designed to fit within a magpie's 'umwelt': association and reversal learning enable magpies to acquire and adjust to predictive contingencies between cues in the environment, including learning from conspecifics and heterospecifics (Ashton et al., 2018; Dawson Pell et al., 2018; Leadbeater, 2015; Morand-Ferron, 2017); inhibitory control is crucial in eliminating immediate but potentially disadvantageous behaviours, such as adaptive responses in both social and asocial contexts (Ashton et al., 2018; Kabadayi et al., 2016); and finally, spatial memory is vital for caching and maintaining territorial boundaries (Ashton et al., 2018; Clayton et al., 2007). While the relevance of caching by magpies can be disputed (*Chapter 2*), there is anecdotal evidence that magpies do cache (Kaplan, 2004), and regardless, spatial memory is utilized to recognize the strict borders that magpies maintain around their territories. For these reasons, the tests used were valid for magpies and provide further support for my findings. However, for future testing, I would suggest modifying the design of this spatial memory task to verify its suitability for magpies.

6.3 | Urban Pollution and Sleep

This thesis provides, to my knowledge, the first evidence that exposure to anthropogenic noise disrupts sleep in wildlife. When exposed to an ecologically relevant noise playback at night, wild-caught Australian magpies slept for shorter durations and less intensely than during a noiseless night (*Chapter 4*).

Once the playback was turned off, magpies continued to show the effects of noise exposure, sleeping more throughout the following night. These results matched predications, providing evidence that anthropogenic noise can have negative impacts on sleep.

This thesis also provides further evidence that light at night affects sleep in wildlife, and supports results from humans that suggest that blue-rich lighting has a greater effect on sleep than does blue-reduced lighting (Ayaki et al., 2016; Van Der Lely et al., 2015). Magpies exposed to part-night lighting in two different colours (blue-rich and blue-reduced) slept less compared to a night of darkness. Once lights were switched off, birds continued to show the impact of the exposure, sleeping for longer, and more intensely throughout the remainder of the night. In addition, birds exposed to blue-rich lighting continued to show altered sleep the following day and night, an effect not seen in blue-reduced lighting. The part-night exposure to light also provided information regarding the effect light has on sleep. Both blue-rich and blue-reduced lighting caused birds to be awake more during the exposure. However, blue-rich lighting may have also caused physiological effects, potentially through the suppression of melatonin, which is noted by an increase in non-REM sleep during the day following blue-rich light exposure. These results matched my predictions that blue-rich lighting would have greater effects on sleep and that these effects would be both visual and physiological.

Does anthropogenic pollution impair sleep in urban wildlife? We are beginning to understand the effects urban pollutants have on sleep. In this thesis, I showed that both anthropogenic noise (*Chapter 4*) and artificial light at night (*Chapter 5*) impact sleep during and after acute exposure. These results are mirrored by recent studies on pigeons (*Columba livia*) and swans (*Cygnus atratus*) exposed to artificial light at night (Aulsebrook, 2019). Such controlled laboratory studies inevitably also have disadvantages. Wild birds may be able to distance themselves from noise and light during sleep and therefore may not experience the same level of pollution I exposed them to (Dominoni et al., 2014; Potvin, 2017). Nonetheless, given the importance of sleep on fitness (Imeri & Opp, 2009; Irwin, 2015), the results presented in this dissertation add further evidence of the potential harms urban pollutants can have on wildlife. When paired together with research on other behavioural and physiological impacts anthropogenic noise (Francis & Barber, 2013; Kunc & Schmidt, 2019; Shannon et al., 2016) and artificial light at night (Gaston et al., 2017; Stevens & Zhu, 2015) have on wildlife, there is a growing need for councils and environmental agencies to investigate better conservation strategies.

Future research investigating how anthropogenic noise and artificial light at night influence sleep should focus on long term impacts, developmental effects, potential fitness costs, and whether differences exist between species.

Studying how long-term exposure affects sleep would allow us to determine how animals adjust to noise and light, and if they are able to tolerate it over time.

This could provide essential information about how the expansion of cities into once-natural spaces affects wildlife and if they are able to adjust to city life. Conducting a study investigating the effects of noise exposure on development is also imperative. Animals exposed to urban pollutants at a young age show physiological differences as compared to animals in a control (Dominoni et al., 2013; Salmón et al., 2016; Schroeder et al., 2012). Such studies could provide valuable information on sleep ontogeny, and if paired with cognitive testing could provide information on the indirect effect these pollutants might have on cognitive development via disrupted sleep.

With few exceptions (Lesku et al., 2012) little remains known about the fitness costs of sleep deprivation in wild animals. Knowing noise and light can impair sleep, there is also a need to investigate what effect these pollutants have on variety of species from different taxa. As stated in *Chapter 5*, there is contradicting evidence regarding the effect of blue-rich lighting on sleep, having a stronger effect on humans and magpies than on mice. These contrasting impacts of blue-rich lighting on humans and magpies, and on mice, emphasize the fallacy of applying a result found in a single species to all taxa and highlights the need for more research on diverse taxa. This consideration should extend to anthropogenic noise as well. Understanding how urban pollutants impact sleep in wildlife should be a focus of conservation work.

While my thesis provides new evidence regarding the impact noise has on cognition and how urban pollutants can impair sleep, there remain two obvious gaps in our knowledge (Figure 6.1). The first is how short- or long-term disruptions to sleep affect cognitive performance. From my thesis, we know that anthropogenic noise and artificial light at night can disrupt sleep (*Chapter 4*). However, whether sleep impairment has cascading effects on cognitive performance is not known outside of studies of humans and laboratory rodents (Colavito et al., 2013; Krause et al., 2017).

The second is how exposure to artificial light at night affects cognitive function. There are plausible putative mechanistic connections between light exposure and reduced sleep, as well as between reduced sleep and impaired cognition. Nevertheless, demonstrations of direct or indirect effects of light at night on cognitive performance in wildlife remain elusive.

6.4 | Concluding Remarks

Urbanization is inevitable. With every passing year, the human population grows, cities expand and areas once natural are developed. The pollutions that accompany urban developments are now seen, heard, and felt in some of the world's most protected and remote areas, and their effects are altering the behaviours of wildlife, in sometimes unpredictable ways. My research demonstrates that anthropogenic noise and artificial light at night – two of the most common forms of urban pollution – can alter sleep in a diurnal bird, which could potentially harm their health and fitness. In line with my predictions, blue-rich lighting was more disruptive to sleep than blue-reduced lighting. Yet while I also expected that anthropogenic noise would impact cognitive function and development, I found little evidence for this.

It is possible that with respect to my findings about the relationship between noise and cognition, Australian magpies will come to represent the exception, rather than the rule. Urban pollutants clearly have the potential to affect biologically important processes via direct and indirect pathways, but systematic empirical verification of each potential pathway will need be undertaken to verify and test assumptions related to these pathways – preferably in multiple species.

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Appendix A: Supplementary materials for *Chapter 3*

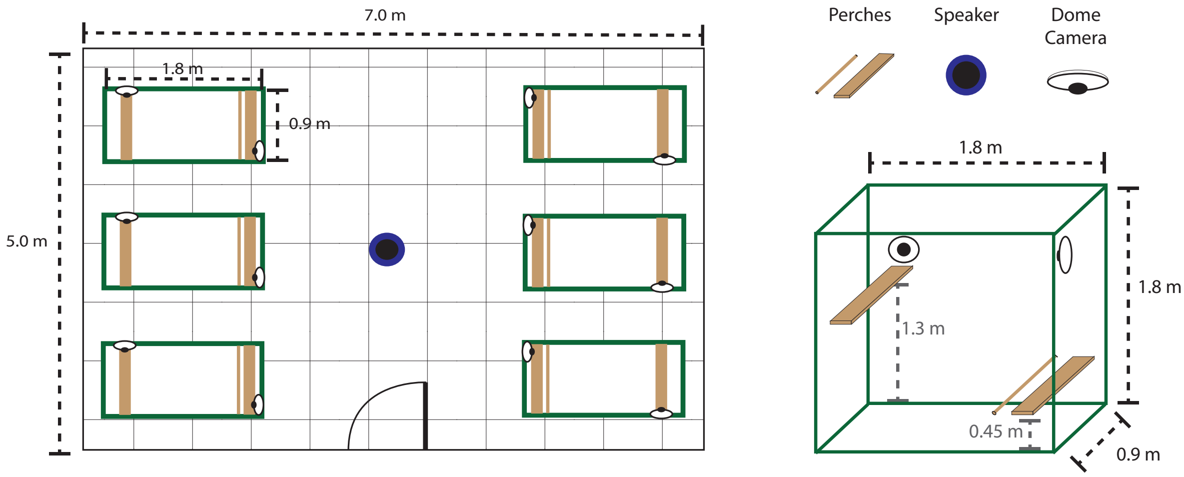


Figure A1. Room setup to investigate the effect of noise exposure on cognition. Room and aviary arrangement; one of the two rooms housed only five magpies.

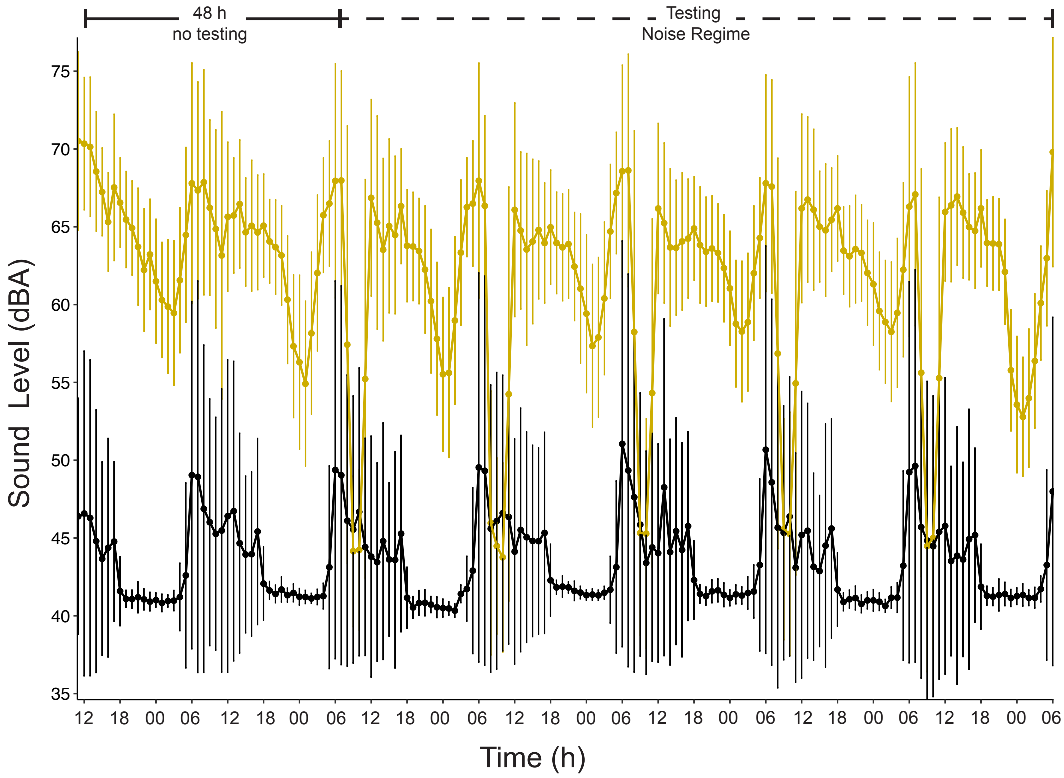
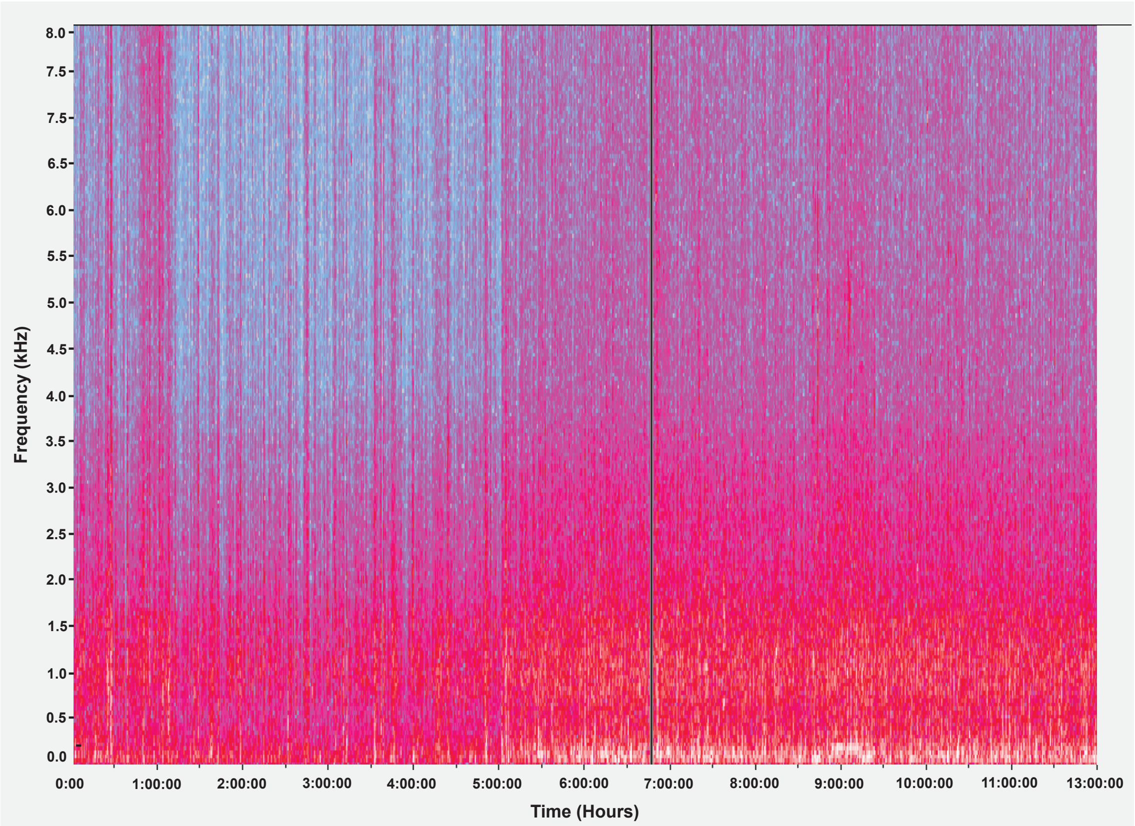


Figure A2. Average treatment sound levels per hour ± SD of the entire seven-day playback over an entire week starting with the 48-hour noise exposure prior to the start of cognitive testing (control: black; noise: yellow). The entire week was played back following the testing noise regime (no noise for 3-h of testing each day). Spikes of noise occurring intermittently across the control reflect carolling.

Figure A3. Sonogram of one 12-h segment (0100 – 1300) of the noise playback.



Appendix B: Supplementary materials for *Chapter 4*

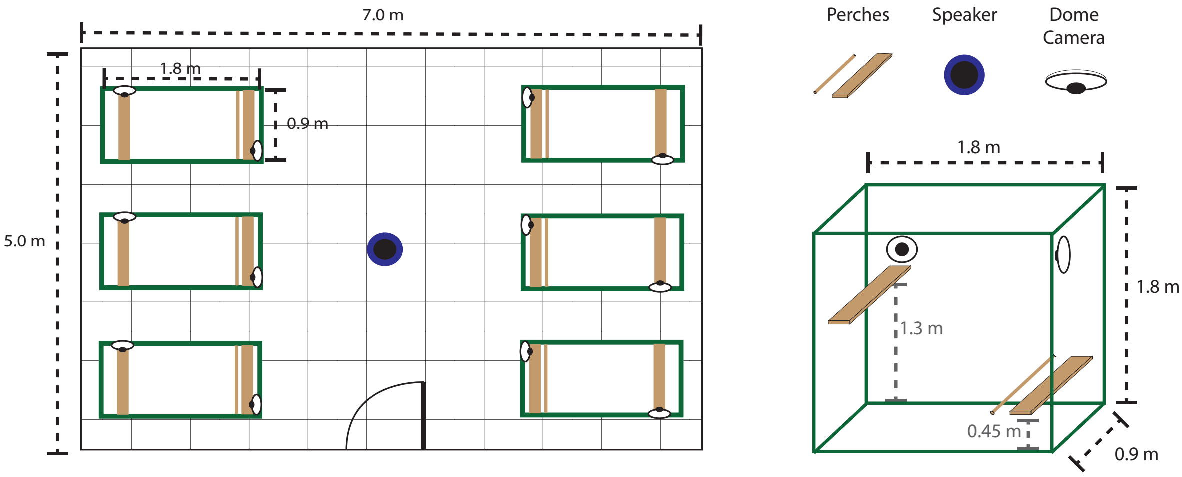


Figure B1. Room setup to investigate the effect of noise exposure on sleep. Room and aviary arrangement; one of the two rooms housed only five magpies.

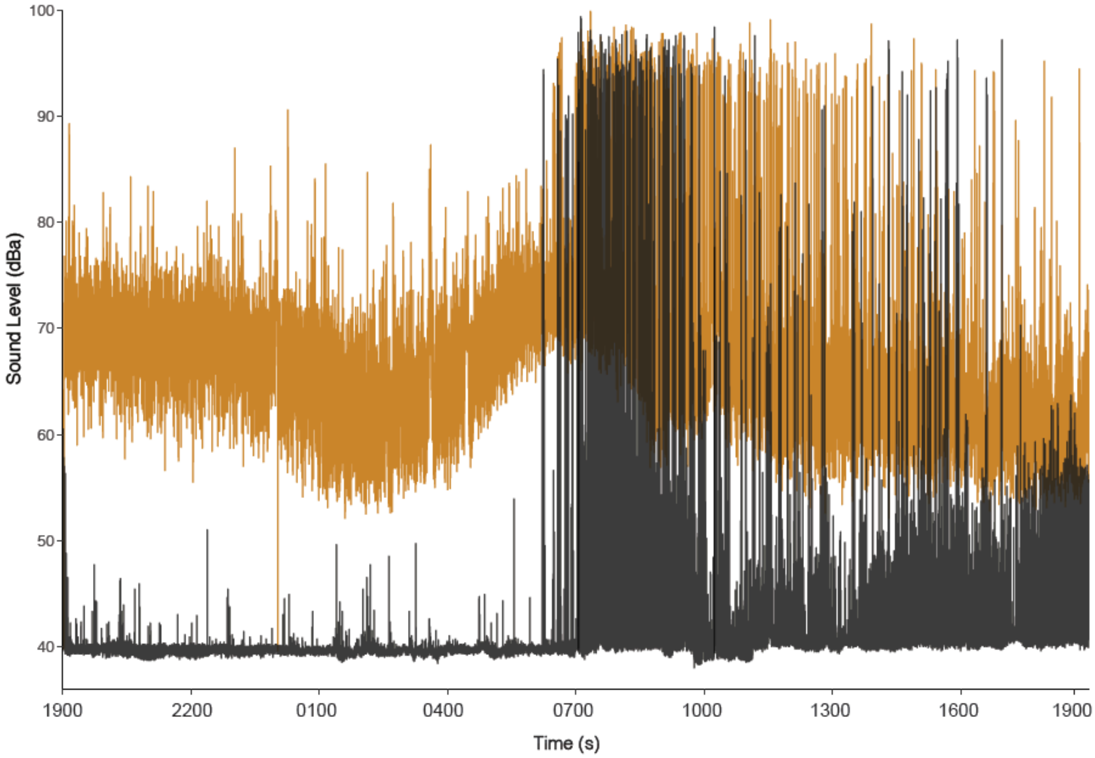


Figure B2. Sound levels during the 24-h control (black) and urban noise playback (orange) days. As intended, the rooms are much louder environments during the noise playback, particularly at night. Spikes of noise occurring intermittently across the baseline day reflect carolling.

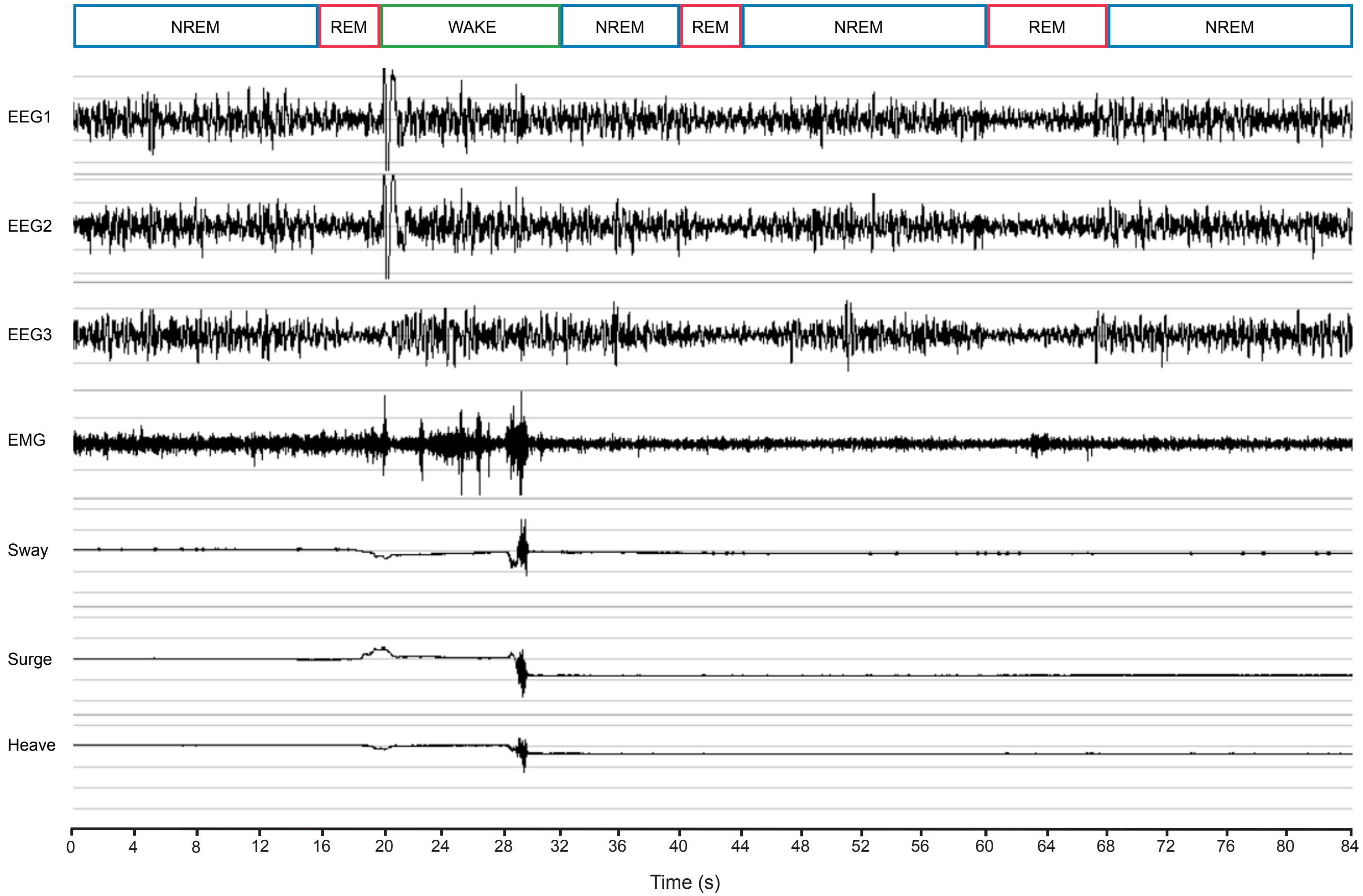


Figure B3. Eighty-four-second example of EEG signals from the left and right hemisphere, neck EMG, and tri-axial head acceleration (sway [lateral], surge [forward/backward] and heave [vertical]) in Australian magpies. EEG signals were filtered to 1 – 20 Hz, a high pass filter of 10 Hz was applied to the EMG, and the acceleration signals are unfiltered

Appendix C: Supplementary materials for *Chapter 5*

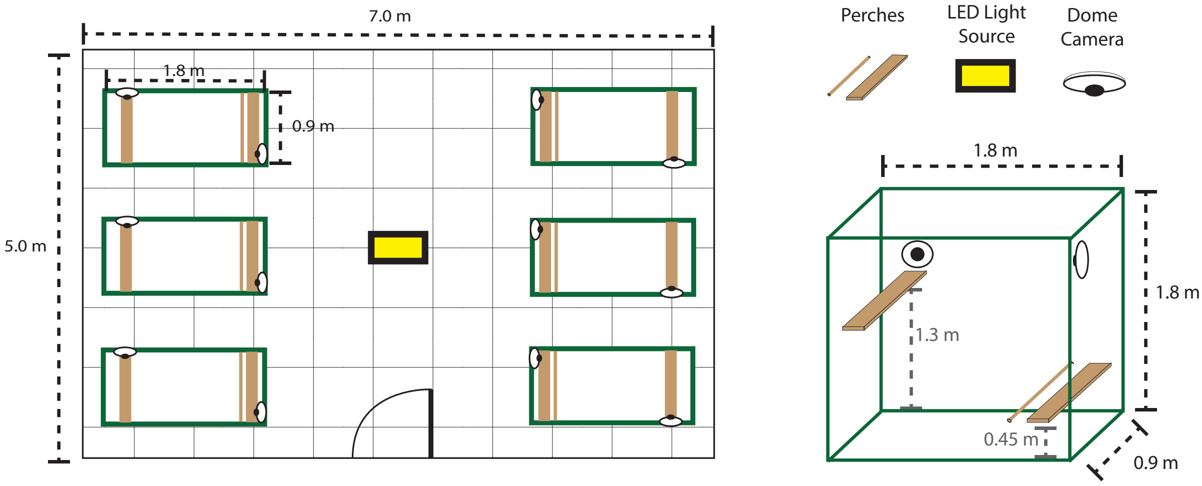


Figure C1. Room setup to investigate the effect of light at night on sleep. Room and aviary arrangement; one of the two rooms housed only five magpies.

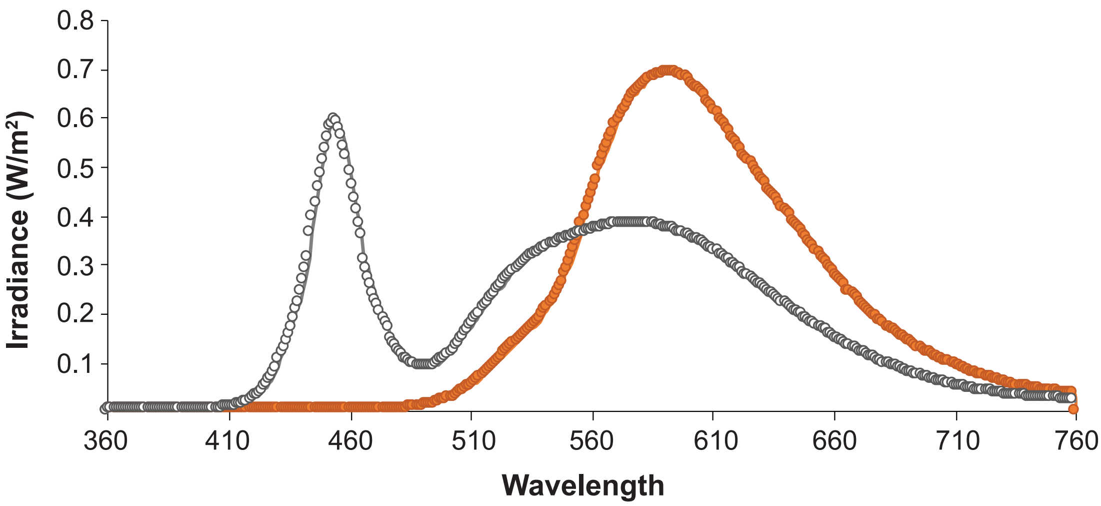


Figure C2. Spectral output of white lighting (white) and amber lighting (orange). Light spectra were recorded at perch height using a MK350 LED Meter (UPRtek Zhunan, Taiwan) 2 m from the light.

Table C1. White and amber lux readings. Lux readings from all 11 aviaries for each light treatment (white and amber). All readings were recorded at the most common sleeping perch (top perch).

Aviary	White lux	Amber lux
01	10.3	11.2
02	10.3	11.2
03	9.4	10.4
04	9.5	8.4
05	11.4	9.9
06	11.4	9.9
07	7.9	10.0
08	7.9	8.4
10	9.8	8.5
11	9.0	9.0
12	9.0	9.0
Avg.	9.6	9.6