

Changes in fear responses of urban birds

**A thesis submitted in partial fulfilment of the requirements for the degree
of Master of Research**

18 October 2018

Kathleen Smiley

**Department of Biological Sciences, Faculty of Science and Engineering,
Macquarie University, Sydney, Australia**

Chapter 2 of this thesis is written in the form of a journal article targeted for Urban Ecology

Declaration

I wish to acknowledge the following assistance in the research detailed in this report:
Robert Harcourt, Benjamin Pitcher and Daniel T. Blumstein who provided comments on the project design and this thesis.

All other research described in this report is my own original work.

All research was conducted under the Macquarie University's Animal Ethics Committee Animals Research Authority # 2018/005 and the Scientific Licence # SL102057 issued by NSW Office of Environment and Heritage.

A handwritten signature in black ink, reading 'K. Smiley' in a cursive script.

Kathleen Smiley

18/10/2018

Contents

General acknowledgements	1
Chapter 1 Wildlife responses to urbanisation and management implications	2
Chapter 2 Changes in fear responses of urban birds	12
Abstract	14
Introduction	15
Methods	18
Study species	18
Study sites	18
Data collection	21
Data analysis	22
Results	24
FID and response intensity	25
Flight initiation after alerting to walker	29
Discussion	30
Acknowledgements	34
References	35
Supplementary data	42
Appendix A: Median FID for all species	42
Appendix B: Animal ethics approval	43

General acknowledgements

I would like to thank my supervisors, Benjamin Pitcher, Robert Harcourt and Daniel T Blumstein for their academic support and mentoring this year. I have learnt so much this year and I am grateful to all of you for helping me to reach this point. In particular, I would like to thank Ben for his patience and calmness, Rob for his positivity and Dan for his expertise in this field.

Thank you to everyone in the Marine Predator Research Group for your support, encouragement and friendliness this year. It has been a pleasure to have been part of this group.

Thank you also to my housemate (Larissa Brisbane) and my bible study group for your kindness, patience, encouragement and prayers throughout this year.

Finally, thank you to my parents (Douglas and Rosemarie Smiley) and my sister (Helen Smith) for your understanding and for keeping me in the family loop even when I was busy.

Chapter 1

Wildlife responses to urbanisation and management implications

Written in the form of a literature review, with full references presented in the combined reference list at the end of Chapter 2.

Non-assessable.

From the Master of Research year guide:

“The draft literature review is only marked by your supervisors, and awarded a satisfactory/unsatisfactory grade. ...the literature review does not contribute to a final grade but it is part of the thesis that forms 90% of your mark.”

Introduction

The world's population is increasing by approximately 83 million people per year (United Nations 2017). The global population is projected to rise to around 9.8 billion by 2050, with the majority of this increase to occur in Africa (United Nations 2017). At the same time, the percentage of people living in urban areas is predicted to rise from around 50% to 66% by 2050 (United Nations 2014). At present, North America has the largest percentage of people living in urban areas (82%), although the majority of the increase in urbanisation will occur in Africa and Asia (predicted increase of 56% to 64% by 2050) (United Nations 2014). As a result, there has been an unheard-of rate of expansion in both the number and size of cities in recent decades (Miranda 2017), with urban land cover predicted to increase between 430 000 km² and 12 568 000 km² by 2030 (Seto et al. 2011).

Changes in urban land cover are a key biological and environmental issue as, globally, urbanisation is the main cause of increasing habitat alteration (Luck 2007, Carrete & Tella 2011). Declines in the quality of natural habitats and changes in animal communities have been recorded as a result of urbanisation (Donnelly & Marzluff 2004). The replacement urban habitats, however, can be complex and contain multiple sub-habitats (Rebele 1994). These new habitats contain novel and open ecological niches (Rebele 1994, Niemelä 1999) that some species adapt to better than others (Luniak 2004) and which will be discussed later in the review. Increasing numbers of studies are examining the responses of wildlife to urbanisation (Magle et al. 2012, Battles et al. 2018), although much is unknown about the mechanisms behind their responses.

One of the issues that is hindering the study of this topic is the lack of consensus on relevant terminology. Some authors, for example, Møller (2010) provide qualitative definitions for urban areas, while others (e.g. Van Donselaar et al. 2018) have a quantitative basis for their definition. However, many studies do not define urban, or other associated terms, such as peri-urban and rural. This issue was identified in McIntyre et al. (2000) and Marzluff et al. (2001 and works cited therein), who also noted that a wide range of terminology is being used, with inconsistent definitions. Despite nearly two decades passing since their publication, this issue appears to remain unresolved. This has implications for a range of issues including wildlife monitoring and management as it can complicate matters when designing and comparing studies (McIntyre et al. 2000).

Synurbanisation

Challenges and opportunities

Landscape changes associated with urbanisation include decreases in vegetation and increases in artificial structures like walls and light posts (Rebele 1994, Battles et al. 2018). The changes in the landscape and corresponding niche availability result in both challenges and opportunities for many species. One of the challenges is that, in a historical sense, urban areas are relatively new environments for species to adapt to (Luniak 2004, Miranda 2017). However, Garcia et al. (2017) argue that it is unlikely that conditions within cities are completely novel. Regardless, it is clear that cities have predominantly been designed to suit humans only (McKinney 2006). In urban areas, species frequently confront selection pressures that differ considerably from those to which they have evolved to suit (Lowry et al. 2013).

Some of these pressures include higher levels of pollution (Kekkonen 2017) and increased levels of disturbance by humans (including pedestrians and vehicles) (Carrete & Tella 2011, Lowry et al. 2013). Opportunities in urban areas arise from features such as new nesting sites, including buildings and birdhouses (McKinney 2006, Clucas et al. 2011) and a milder microclimate (Luniak 2004). Perhaps the greatest influence on urban birds is the availability of human sourced food (Fidino & Magle 2017), including bird feeders (DeStefano & DeGraaf 2003), garbage (Sol et al. 2017) and landfill sites (Martin et al. 2010) that provide food security (Bateman & Fleming 2012) and artificial water sources which do not seasonally fluctuate (Bradley & Altizer 2007, Lowry et al. 2013).

The result of these challenges and opportunities is that some species will be effectively barred from urban areas, while others adapt to the available niches (Møller 2009, Lowry et al. 2013). While urban areas can function as an “ecological vacuum” that is attracting increasing numbers of wildlife (Luniak 2004), urbanisation is a major contributor to biotic homogenization (McKinney 2006). At high levels of urban development, wildlife density (Aronson et al. 2014) and species richness have been found to decrease for some taxa, including birds and butterflies (Blair 1996, Blair & Launer 1997, Lee et al. 2004). However, there is evidence that this does not occur uniformly, with other species such as wild bees and birds of prey being recorded in higher abundance in urban than non-urban areas (Banaszak-Cibicka & Żmihorski 2012, Fischer et al. 2012).

Synurbic species

This range of responses in urbanisation led to the development of names for the three different responses: avoidance, adaptation and exploitation, as reportedly coined by Blair (Blair 2001 as cited in McKinney 2006). Both adapters and exploiters can adjust well to urban areas, but the latter thrives in such environments and can become reliant on the resources in urban areas (McKinney 2006). Establishment of exploiter species in urban areas is increasing, which has led to the development of the term synurbanisation (also referred to as synanthropisation) and associated terminology (Andrzejewski et al. 1978, Luniak 2004). Specifically, synanthropic refers to wildlife that adjust to the particular conditions found within urban areas (Andrzejewski et al. 1978, Luniak 2004), with synanthropic species “associated with humans” and human habitation and synurbic species associated with urban areas (Francis & Chadwick 2012). To be counted as synurbic, exploiter species must associate more with urban areas than other ecosystems (Francis & Chadwick 2012). This may be an important adjustment as synurbanisation can be considered to be one of the responses of wildlife to increasing urbanisation (Luniak 2004). However, these three responses could lead to geographical separation of populations along the lines of the three responses, further to disconnected populations with the associated issues, including gene flow (McKinney 2006).

There are at least three main factors that increase the likelihood that an animal will become synurbic, which are broadly summarised in Sol et al. (2017). Firstly, a broad ecological niche, where generalists are highly successful (Carrete & Tella 2011). Secondly, phenotypic plasticity, including behavioural flexibility (Luniak 2004, Garcia et al. 2017). Lastly, tolerance towards humans (Luniak 2004, Carrete & Tella 2011). In this regard, the tameness levels of individuals, rather than that of the species may be more influential in determining which species invade urban areas (Carrete & Tella 2011). However, much is still not understood about the mechanisms behind species adapting to urban environments and how urban ecosystems function (Carrete & Tella 2011). Further, most research to date appears to be on species invading urban areas and native species leaving urban areas, with less attention given to local and native species that adapt to the urban environment.

Synurbic species including geese (DeStefano & DeGraaf 2003), the Australian white ibis (*Threskiornis molucca*) (Martin et al. 2007), coyotes (*Canis latrans*) (Timm et al. 2004) and raccoons (*Procyon lotor*) (Riley et al. 1998) have been shown to be capable of achieving high urban population densities. This can result in species exceeding an area’s “cultural carrying capacity” (Ellingwood & Spignesi 1986 as cited in Carpenter et al. 2000), that is, what a human population will tolerate as an acceptable number (DeStefano & DeGraaf 2003). At this point, the animals can

cause economic, environmental and/or social problems (DeStefano & DeGraaf 2003), which results in many such species being considered pests (DeStefano & DeGraaf 2003, Smith 2009).

Habituation and sensitisation

Changes in tolerance towards humans (and other animals) are referred to as sensitisation or habituation. Habituation is defined as a decrease in behavioural response due to reoccurring stimuli that is not due to sensory and motor adaptation or fatigue (Rankin et al. 2009). Habituation can be advantageous as it reduces the likelihood that individuals will spend time and energy needlessly responding to stimuli that do not pose a threat to the animal (Blumstein 2016). For example, it has been suggested that habituation towards humans can result from regular and slow approaches from people who do not attack or harass the animal (Weston & Elgar 2007). The speed at which habituation occurs can vary, with some species going rapidly through this process while others habituate more slowly (Guay et al. 2016). Animals can also increase their response to a reoccurring stimuli, which is known as sensitisation (Blumstein 2016). As with habituation, this process can be beneficial if it allows animals to avoid situations which may have risks or costs associated with it (Blumstein 2016). Animals can also become dishabituated, which is one type of sensitisation, which can occur when the stimuli is removed (Groves & Thompson 1970).

The extent to which an animal will habituate or sensitise is not always clear, although it is not an indefinite process (Blumstein 2016) and responses may decrease or increase in an asymptotic fashion (Rankin et al. 2009). Additionally, changes in tolerance may not always be in a single direction, that is, habituation may follow after an initial sensitization response or vice versa (Groves & Thompson 1970). An interesting note is that high tolerance of Antarctic seabirds towards humans could reflect the natural tolerance levels of some species and that the lower tolerances at other locations could be due to predation by humans (Nisbet 2000). This means that, in some circumstances, current observations of habituation may actually be a reversion towards the original level of tolerance (Nisbet 2000). To determine whether habituation or sensitisation has occurred, known individuals would have to be repeatedly observed over time which is not always a possible, or viable, option (Bejder et al. 2009, Blumstein 2016). However, population level changes in tolerance have been recorded for species such as whales where it is not always possible to distinguish individuals (Watkins 1986). The barrier to better understanding these processes is that most studies have only examined habituation in the short term (Jack et al. 2008) and sensitisation and dishabituation have been studied even less (Groves & Thompson 1970).

Flight initiation distance (FID)

Assessing behavioural habituation is often done by measuring anti-predatory behaviour responses, such as flight. The distance at which an animal flees from a potential predator is called the flight initiation distance (FID) (Ydenberg & Dill 1986). FID is collected as a measure of disturbance and risk taking as animals often flee and/or hide from potential predators (Møller 2009, Blumstein 2016). FID is a useful tool for quantifying how an animal views different predation risks and provides important information for the management of wildlife (Blumstein 2016). This is partly because FID is seen as a standardised method that is highly repeatable between researchers (Cooper Jr et al. 2008). It has also been used on a range of animals, including fish (e.g. Rhoades et al. 2018, Sbragaglia et al. 2018), amphibians (e.g. Rodríguez-Prieto & Fernández-Juricic 2005, Ozel & Stynoski 2011), reptiles (e.g. Layne Jr & Ford 1984, Cooper Jr et al. 2008), birds (e.g. Blumstein et al. 2003, Guay et al. 2013) and mammals (e.g. Dill & Houtman 1989, Bonenfant & Kramer 1996), highlighting the broad applicability of this method.

Factors that affect FID

While there are a number of benefits in using FID, there are several factors that need to be considered when collecting and analysing the data. For example, the starting distance (SD) for the approach is positively correlated with FID (Blumstein 2003, Cooper Jr et al. 2008) and anthropogenic noises, such as boat motors, can distract or prevent animals from detecting the approaching human (Chan et al. 2010). Characteristics of the animal, such as reproductive status (Cooper Jr et al. 2008), group size (Fernández-Juricic et al. 2002), availability of resources, and distance to a refuge (Dill & Houtman 1989, Stankowich & Blumstein 2005, Guay et al. 2013) can influence FID. Animals may also detect a potential threat before displaying an overt reaction (Chamailé-Jammes & Blumstein 2012), which can be associated with a physiological response such as increased heart rate, as recorded in Adélie penguins (*Pygoscelis adeliae*) (Giese 1998). By understanding the factors that affect and interact with FID, researchers can better predict how anti-predatory behaviour can vary in relation to them (Blumstein 2006).

FID and urbanisation

An increasing number of studies are examining the effects of urbanisation on birds (Marzluff et al. 2001). Birds are an ideal group to study as they are easily observable, provide important ecosystem services, and can function as indicator species (Lepczyk et al. 2017). A number of studies have compared the FID of rural and urban populations, revealing differences between populations of the

same species (as summarised in Cooke 1980, Møller 2009, 2010, Carrete & Tella 2011). Similarly, Møller (2010) reported a positive correlation between rural and urban FIDs in relation to time since urbanisation. However, in Møller (2010) the date of colonisation was based on observations recorded by contemporary ornithologists and changes in FID were based on contemporary rural FIDs. So, while this study provides an interesting perspective, its interpretation requires caution and it does not provide evidence of chronological changes in FID in relation to urbanisation.

Management Implications

Is habituation beneficial?

The definition of habituation does not indicate either beneficial or adverse consequences (Bejder et al. 2009). This is an important consideration as habituation can be either a desired or an unwanted outcome for wildlife and project managers. A positive effect of habituation is that it can limit the negative effects of human disturbance on wildlife (Nisbet 2000). For example, where human-wildlife contact is unavoidable, such as the development of new walking tracks, habituation may mitigate disturbance (Nisbet 2000, Blumstein 2016). Deliberate habituation of animals by using taming processes have also been used on wildlife such as apes to improve accessibility for researchers and tourists (Johns 1996, Woodford et al. 2002). However, there are situations where habituation is an undesirable outcome. Habituation can reduce the effectiveness of pest control programs (Baxter & Allan 2008) and increase human-animal conflict (Madden 2004). This can result in dramatic increases in the cost and duration of control programs and lethal measures being used to control or remove the animal/s at the centre of the problem (Madden 2004, Baxter & Allan 2008). An important consideration is that habituation can transfer from benign human activity to possibly lethal activities, such as hunting and other hazards (such as vehicular activity), potential predators (Bejder et al. 2009 and references therein) and poaching (Ménard et al. 2014). Given the consequences, activities and management plans should take the range of potential outcomes into consideration, ideally in advance (Bejder et al. 2009).

Consequences of disturbance

Regardless of whether habituation is desirable or not, there are still costs associated with the process. For example, reproductive success can decrease as some species, for example, penguins and masked lapwings, may desert their nests (Weston & Elgar 2007, Pichegru et al. 2016). Time spent foraging can decline if the animal spends increased amounts of time being vigilant of humans

(Fernández-Juricic & Tellería 2000). Possible outcomes of this are that areas become less suitable for some species (Fernández-Juricic 2000) and shyer individuals may leave the area (Pichegru et al. 2016). Given the range of possible consequences, it is important to identify ways to reduce or avoid the amount of human disturbance that animals are exposed to, especially in the context of the increasing world population and urbanisation (Tätte et al. 2018).

Science into policy

Data availability

The purpose of many studies on the effects of human activities on animals is to provide a scientific foundation for wildlife management (Stankowich & Blumstein 2005, Bejder et al. 2009), such as the creation of suitable buffer zones (Weston & Elgar 2007). FID and similar data can be used to justify the need for buffer zones as well as their size (Fernández-Juricic et al. 2005). Understanding the assumptions and applicability of data collection methods is important for designing buffer zones (Fernández-Juricic et al. 2005). Failure to do so can lead to inappropriate sizing, which can either over- or under-regulate human activity in and around these areas. These biases may be heightened due to publication bias arising from researchers only submitting significant findings (Carney & Sydeman 1999), higher rejection rates from scientific journals for non-significant results of negative or positive results, researchers selecting species where humans are likely to have greater impact (Luck 2007) and negative results being less frequently published, regardless of whether the results were statistically significant or not (Frid & Dill 2002).

Suitable information on flight responses of animals is often limited, or not available (Weston & Elgar 2007). Current limitations on information include the number of locations and species that have been sampled, the length of studies, and types of disturbances investigated. Geographically, most studies are from the Northern Hemisphere (Lepczyk et al. 2017) and the majority have been done in temperate forests (Marzluff et al. 2001). Few studies have investigated flight responses of migratory species, which is important as settling in an urban area is not an option for some species (Garcia et al. 2017). Information on migratory species is needed to ensure that buffer zones and other conservation tools are adequate to protect both resident and migratory species (Mikula et al. 2018).

Interspecific differences are also important as they can affect the distribution and abundance of a species, and its ability to adapt to changes in environmental conditions (Blumstein 2006). Due to practicality and financial limitations, most studies measure behavioural responses in the short-term

and with non-known individuals (Bejder et al. 2009). Typically, studies on the response of avian species to urbanisation only last one or two years (Marzluff et al. 2001). Combined, the typical short duration of studies and low number of studies on known individuals means it can be difficult to understand the mechanisms of how wildlife respond to disturbance. There are also limited variations on the type of disturbance used for the study, with most FID studies using a single walker, which does not always reflect reality (Weston & Elgar 2007). While this makes studies comparable, it does leave many gaps in our understanding of flight reactions to a range of situations. More information about what types of activities cause the most disturbance is needed (Carney & Sydeman 1999), as is information about intraspecific variation (Blumstein et al. 2003). It is important to address these gaps as “only rigorous science is likely to produce well-informed, effective public policy” (Marzluff et al. 2001).

Data applicability and importance

FID and similar data can be of interest to people concerned with the effects of habituation and urbanisation. This includes animal welfare supporters, conservation managers and policy makers (Marzluff et al. 2001, Guay et al. 2016). Transferring knowledge between the different groups is important, although often not a smooth process (Roux et al. 2006). Results published in journals may not be easily accessible, and so translating them into something that different groups can apply may be difficult (Kochert & Collopy 1998), as the results may be complex and include considerable uncertainty (Kochert & Collopy 1998). Compounding this problem is that even if data exists, there is no main repository for such information (Weston et al. 2012). Tools such as AvianBuffer, (an online tool which provides estimates of FID for Australian birds, based on recorded observations), may help to address this issue (Guay et al. 2016). Improved communication and collaboration between researchers, wildlife managers, planners and policy makers may improve management strategies (Kochert & Collopy 1998, Madden 2004). Establishing communication and collaboration is also important to ensure that management plans are realistic, and avoid expectations that are unrealistic, and the creation of unmanageable numbers of poorly designed management plans, which could result in the failure of some, or all of these plans (Agardy et al. 2003, Pomeroy et al. 2005). As such, the challenges of creating and maintaining a management area, or managing a species, are many and these need proper consideration (Pomeroy et al. 2005).

Support for management plans

Wildlife managers need to balance wildlife needs against the needs and “social wellbeing” of the public (Madden 2004). Public consultation can be important in creating buffer zones to ensure that there are “socio-politically, as well as ecologically, sustainable outcomes” (Guay et al. 2016).

Obtaining public and industry support is essential as a well-designed management plan is ineffective if there is limited or no compliance. Management plans need to be well-constructed and include mechanisms to allow for adjustments as new information becomes available. Ongoing monitoring is needed to help ensure that the plans meet their objectives (Pomeroy et al. 2005), although funding could be a considerable limitation to this. FID and similar studies can be used to determine the effectiveness of protected areas, hence researchers may need to stay connected to the management plan long after it is created (Kochert & Collopy 1998). In this regard, baseline data is important (Kochert & Collopy 1998) as is an understanding of ongoing urbanisation and the changing behaviour of wildlife in response to it.

Chapter 2

Changes in fear responses of urban birds

Written in the form of a journal article targeted for Urban Ecology, with a combined reference list at the end of the chapter

Changes in fear responses of urban birds

Kathleen Smiley^{a*}, Robert Harcourt^a, Daniel T. Blumstein^b and Benjamin J. Pitcher^{a,c}

^aDepartment of Biological Sciences, Macquarie University, Sydney, NSW, 2109, Australia

^bDepartment of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1606, U.S.A.

^cTaronga Conservation Society Australia, Mosman, NSW, 2088, Australia

*Corresponding author. Email: kathleen.smiley@hdr.mq.edu.au

Abstract

Wildlife will often modify their behaviour when disturbed by humans. The distance at which animals flee from humans (flight initiation distance (FID)) generally decreases along the rural-urban gradient and as a function of time since the species' colonisation. However, no known studies have monitored the ongoing responses of birds to urbanisation. To see how urban birds have responded to increasing urbanisation and how this varied between sites, I undertook an FID study at sites where FID had been measured in 2000. I examined how FID, response intensity (proportion of birds that walked away), and delays in flight after detecting the walker differed between the two periods, focusing on four species with the most observations. I found that in 2018, silver gulls (*Chroicocephalus novaehollandiae*) had significantly reduced FID both overall, and at the high disturbance sites, although there was no difference in response intensity. As expected, silver gulls and the Australian white ibis (*Threskiornis molucca*) also generally delayed flight more after detecting the walker in 2018 than in 2000. While species' responses in the intervening years are unknown, these results suggest that these two species are responding to increasing urbanisation presence, while the masked lapwing (*Vanellus miles*) and pied oystercatcher (*Haematopus longirostris*) are not. The exploiter species (silver gulls and the Australian white ibis) were frequently encountered in situations where human-sourced food was available, and hence delaying flight would often have been beneficial, while it was less advantageous for the other two species to delay flight as they were generally utilising natural resources.

Keywords: Urbanisation, anti-predator behaviour, flight initiation distance (FID), human-wildlife interactions, urban birds, phi index

Introduction

Globally, urbanisation, environmental alteration associated with urban development (Luniak 2004), is a major cause of ecosystem change (McKinney 2002). Alterations include the removal of habitats and permanent changes to the landscape, such as decreases in vegetated areas, increases in artificial structures and impervious surfaces (Blair 1996, Pauleit et al. 2005), as well as habitat fragmentation (Shanahan et al. 2014). The effects of urbanisation are of concern because the world human population continues to increase and populations within urban areas are growing at a faster rate than rural areas. Currently there are around 7.5 billion people globally and it is estimated that this will reach around 9.8 billion by 2050 (United Nations 2017). Already more than 54% of people globally live in urban areas and this is expected to increase to 68% by 2050 (United Nations 2014). Increasing populations and urbanisation combined are generating a rapid expansion in the number and size of cities (Miranda 2017). This expansion will cause an estimated additional 1.5 million km² of rural land to be converted to urban land by 2030 (Seto et al. 2011).

Urban landscapes create both challenges and opportunities for wildlife as they contain novel and open ecological niches (Rebele 1994, Niemelä 1999, Luniak 2004). Challenges from habitat transformation include habitat loss (Shanahan et al. 2014), higher levels of pollution and increased levels of human disturbance (Blair 1996, Carrete & Tella 2011, Lowry et al. 2013). Conversely, new opportunities may arise from the artificial features in urban structures providing new nesting sites (McKinney 2006, Clucas et al. 2011), or a milder microclimate (Luniak 2004). Some urban wildlife may have increased food security from human sourced food (Bateman & Fleming 2012), including bird feeders (DeStefano & DeGraaf 2003), direct feeding (Warren et al. 2006), garbage (Sol et al. 2017), landfill sites (Martin et al. 2010) and artificial water sources (Bradley & Altizer 2007, Lowry et al. 2013). The responses of species to these challenges and opportunities will determine whether they will decline in abundance or disappear completely from urban areas, or be able to adapt to and thrive in the available ecological niches (Møller 2009, Lowry et al. 2013, Shanahan et al. 2014).

Wildlife can respond in three ways to the challenges and opportunities present in urban areas: avoid, adapt or exploit (Blair 1996). Animals which avoid urban areas (avoiders) are unable to adjust to landscape changes and will disappear from urban areas (Blair 1996, McKinney 2006). Other animals can adjust to urban areas, and either use natural resources (adapters) or prosper through exploiting urban resources (exploiters) (Blair 1996, McKinney 2006). Adapters and exploiters come from a range of taxa including butterflies (e.g. fiery skipper, *Hylephila phyleus* and spring azure, *Celastrina ladon* (Blair & Launer 1997)), mammals (e.g. coyotes, *Canis latrans* (Timm et al. 2004),

raccoons, *Procyon lotor* (Riley et al. 1998)) and birds (e.g. silver gulls, *Chroicocephalus novaehollandiae* and the Australian white ibis, *Threskiornis molucca* (Martin et al. 2010)).

An increasing number of animals are becoming established in urban areas and the terms synanthropisation and synurbanisation are often used to describe the process of adjustment that these species go through in their colonisation of these areas (Luniak 2004). Luniak (2004) defines synanthropic as animals that adapt generally to conditions that are created by humans and synurbic as a subcategory of synanthropic, where wildlife have adapted specifically to the conditions that are in urban environments (adapter and exploiter species). Synurbic species are an extreme case of synanthropisation, where the animals associate more with urban areas than other ecosystems (Francis & Chadwick 2012) (exploiter species only). Synurbic species occupy a broad ecological niche, where generalists are highly successful (Carrete & Tella 2011). High levels of behavioural flexibility are also common, with adapter and exploiter species adjusting behaviour to suit the conditions found in urban areas (Lowry et al. 2013) and showing increasing tolerance towards human disturbance (Carrete & Tella 2011).

Measuring behavioural tolerance is often done by quantifying anti-predatory behaviour and fear responses. Flight initiation distance (FID; Table 1) is a useful tool to quantify how animals assess predation risk and provides important information for managing wildlife, including birds (Blumstein 2016). FID is a standardised method that is highly repeatable between researchers (Cooper Jr et al. 2008) and data are relatively easy to collect (Stankowich & Blumstein 2005). The collection of FID also includes measuring the starting distance (SD) and often the alert distance (AD; Table 1). SD and AD are frequently correlated with FID (e.g. Blumstein 2003, Samia et al. 2013) and the flush early and avoid the rush (FEAR) hypothesis suggests that the AD-FID relationship exists because birds will flee early to avoid ongoing monitoring costs (Blumstein 2010).

Table 1. Definitions of terms used in the text (modified from Cooper Jr & Blumstein 2015)

Term	Definition
starting distance (SD)	The straight-line distance in metres between the human walker and the bird when the walker starts moving towards the bird
alert distance (AD)	The straight-line distance in metres between the human walker and the bird when the bird first shows overt notice of the human walker by a change in posture or head orientation
flight initiation distance (FID)	The straight-line distance in metres between the human walker and the bird when the bird first moves away from the human walker by walking or flying

Fear responses in birds are known to vary in relation to levels of human disturbance. For example, studies have shown that avian FID often decreases along the rural-urban gradient (e.g. Rollinson & Jones 2006, Díaz et al. 2013, Samia et al. 2017). Tätte et al. (2018) found that the SD-FID relationship was stronger in rural than urban areas, which they attributed to higher levels of noise and visual stimuli in urban environments. AD-FID has also been shown to be weaker in urban than in rural areas (Samia et al. 2017). FID has also been shown to decrease as a function of time since colonisation of an urban area by avian species, when comparing contemporary rural bird FID to that of their counterparts in urban areas (Møller 2010). This suggests that birds may adjust their fear responses continuously within an area where increasing urbanisation is occurring. However, to date, I am aware of no studies that have measured FID on the same species at the same sites, over time, as urbanisation has increased. Such a study would provide a direct empirical assessment of how urbanisation directly influences fear responses.

In this study, I investigated whether urban birds in Sydney, Australia have responded to increasing urbanisation. Blumstein et al. (2003) previously investigated urban bird FID in this area in 2000 and found that it was a species-specific trait, with eight urban bird species displaying a relatively consistent FID across six sites with varying levels of disturbance (Table 2). Since 2000, the population of Sydney has increased by approximately 1.2 million to reach 5.1 million (Australian Bureau of Statistics 2018) and is expected to reach 7.4 million by 2046 (Infrastructure Australia

2018)). Population growth in this area is continuing to result in an expansion in landcover area and increased housing density (Infrastructure Australia 2018).

I revisited each of the six sites studied in 2000 and assessed how FID had changed for the same species in the intervening 18 years and asked the following two questions. First, are urban birds responding to changes in urbanisation and does this vary by species? Second, how do responses and change in response vary between sites with different levels of disturbance? I used the data collected in the original study and this study to compare fear responses by examining FID, response intensity (the proportion of birds that walked away, a low intensity response) and AD-FID relationship in 2000 and 2018. As these types of fear responses are often less marked in areas where there are a) higher levels of human disturbance and b) as a function of time since urbanisation, I predicted first, that FID and response intensity would have decreased, and secondly, that the AD-FID relationship would be weaker in the 2018 period than in the 2000 period. I also expected that any differences would be greater a) for the white ibis which has undergone recent population increases and is known to utilise anthropogenic food resources in this area (Martin et al. 2010) and b) at the more disturbed sites as urban challenges and opportunities may be greater there, potentially putting more pressure on individual birds to adjust their fear response than at the less disturbed sites.

Methods

Study species

I collected data on the same original eight bird species as those in Blumstein et al. (2003), namely the Australian pelican (*Pelecanus conspicillatus*), Australian white ibis (hereafter ‘white ibis’), bar-tailed godwit (*Limosa lapponica*), crested tern (*Sterna bergii*), masked lapwing (*Vanellus miles*), pied oystercatcher (*Haematopus longirostris*), silver gull, and white-faced heron (*Ardea novaehollandiae*).

Study sites

I collected data at all six of the original sites (Blumstein et al. 2003) for each of the eight species where they were present. These six sites are located around the coastal edge of Botany Bay, Sydney, Australia (34°00’S, 151°13’E): Penrhyn, Kyeemagh, Sandringham, St George Sailing Club, Taren Point and Towra Point Nature Reserve (Figure 1). Site impact levels (low, moderate or high disturbance) were assigned to each site by ranking them according to their degree of

urbanisation (Table 2). This was a qualitative assessment based on the number of people present at each site, activities taking place and the number of developments at, or close to, the site during the study period. No quantitative information on visitor numbers was available from either the original thesis (L. Anthony 2000 unpublished honours thesis) or the published paper (Blumstein et al. 2003). While the population of this area has increased, the nature of the disturbance has changed very little.



Figure 1. Map of the six study sites located around the edge of Botany Bay, Sydney, Australia with reference to site disturbance levels (low, moderate and high)

Table 2. Classification of low, moderate and high disturbance levels

	Low	Moderate	High
human presence	Very few or no people around at the site	Some people at the site, mostly just passing through the site	Moderate to high numbers of people throughout the site, with some people lingering within the site and opportunities for exploiter species to scavenge food
built environment	Very few or no buildings and/or roads at the site	Some buildings, roads or facilities at the site	Moderate to high number of buildings, roads or facilities at the site

Penrhyn, Kyeemagh, Sandringham and St George Sailing Club were classified as highly disturbed sites (Figure 1). Penrhyn is situated between Port Botany and Australia's busiest airport (Sydney Kingsford Smith Airport) (Department of Infrastructure 2018). In 2000, the site was a mix of sandy and muddy beaches with two boat ramps and a pier that was used for recreational fishing and was highly polluted. Since 2000, this site has undergone major physical changes. Port Botany has been expanded through land reclamation, with habitat enhancement works subsequently undertaken within Penrhyn Estuary (Cardno 2018). Due to post-construction habitat protection it was not possible to enter the upper estuary in 2018 and observations were restricted to the foreshore section of the original Penrhyn site. The original boat ramps and pier have since been replaced by a single large boat ramp and a large car park has been built adjacent to the boat ramp.

Kyeemagh is a public sandy beach area located on the other side of Sydney Kingsford Smith Airport to Penrhyn. In 2000, the site had a park area with a picnic area and playground and was bounded by a busy road. The site also contained a rock jetty and netted swimming area used by recreational fishers and swimmers, and a kiosk. Since 2000, this site has generally changed little, although individual features have been updated. These features include the expansion of the picnic area and playground and the original car park being replaced by two separate car parks.

Sandringham is a public sandy beach with a park area, south of Kyeemagh. In 2000, the site contained a busy walking path near the beach and a netted swimming area. Since 2000 this site has changed very little. It still has a busy pathway used by walkers and cyclists and contains picnic areas, playgrounds and a kiosk that were also present in 2000. St George Sailing Club is a highly tidal, public sandy beach with a park area that are separated by a residential street. In 2000, the site

contained sand dunes between the shoreline and the road, a playground and a busy walking pathway and fishers were seen on the beach collecting fresh bait. Since 2000, the site has changed very little, although a creek on the boundary of the site (Bado-berong Creek) has undergone habitat enhancement works.

Taren Point was classified as a moderately disturbed site (Figure 1). Taren Point is a small park area with a mix of sandy and muddy beach and highly tidal shoreline. In 2000, this area had a grassy area between the shoreline and adjacent medium density housing. Since the original study the site has been rehabilitated, including establishing a saltmarsh community as a buffer between the shore and a shared pathway that is in a recreational reserve (Whitfield 2011). The reserve section of this site has become a shorebird reserve where dogs are banned from entering, although people were frequently observed bringing their dogs into this area. Taren Point contains a shorebird community (including the masked lapwing and pied oystercatcher) that was listed in 1998 as an Endangered Ecological Community (Office of Environment and Heritage 2011).

Towra Point Nature Reserve was classified as a low disturbance site (Figure 1). The reserve is managed by New South Wales National Parks and Wildlife Service (NPWS). This site is a highly tidal sandy beach east of Taren Point and permission from NPWS is required to access this land. In 2000, this site was sheltered from the nearest road by a thick vegetation barrier and people were spotted riding horses. Since 2000, this site has changed very little and while no horses were seen, several dogs were sighted during 2018.

Data collection

To align with the original fieldwork period, fieldwork took place from 20 April to 29 May 2018 and between 0650 and 1640 Australian Eastern Standard Time. I collected the data following the protocol in the original study (Blumstein et al. 2003) to ensure that the results were comparable as factors such as approach speed and avian behaviour at the time of the approach are known to influence FID (Stankowich & Blumstein 2005). Prior to every approach, I observed the birds from a distance to ensure that they were not disturbed by the presence of the observer (myself) (hereafter 'the walker') or other area users and were engaging in normal activities such as resting or foraging. I approached the birds at a slow, constant pace of between 0.5-1.0m/s and dropped markers at the SD, AD, FID and at the original position of the bird.

After the approach, the distance between each of the markers was measured using a measuring tape and I recorded whether the bird's response was to fly or walk away (the response intensity, which was recorded as flew away = 0 and walked away = 1). As markers were only dropped when I was confident that the bird's response was correctly identified, observations always included SD, FID and whether the bird flew away or walked away, but not always AD. The main observer in 2000 and the only observer in 2018 were similar in height and appearance (drab clothing, dark hair). The intent was to minimise any indirect biases introduced by walker difference, acknowledging that FID in black swans (*Cygnus atratus*) is reportedly not influenced by variability in walker height (Van Dongen et al. 2015).

Since birds were not marked during this study, some individuals may have been approached more than once. While pseudoreplication has been found to not be an issue for yellow-bellied marmots (*Marmota flaviventris*) (Runyan & Blumstein 2004), I visited sites a maximum of once per day to reduce the probability of multiple flushes on individuals within a day. Birds approached were either not part of a group or were in a position within a group where their reaction could be clearly identified. Multiple observations during each site visit were only made if the birds had not seen any of the previous approaches that day. To avoid time of day bias (which has been shown to influence avian FID (e.g. Piratelli et al. 2015)), the order that sites were visited was varied each day, allowing observations to be collected at different times throughout the day.

Data analysis

I compared 2000 and 2018 FID, response intensity (the proportion of birds that walked away), AD-FID relationship to see how these birds responded to urbanisation and whether this varied between sites of different disturbance levels. Visual inspection of the distributions of FID and SD showed that these variables were left skewed and so were \log_{10} -transformed as there were no zeros in the data. The effects of the \log_{10} -transformation were visually checked and revealed that the \log_{10} -transformation of FID and SD of the white ibis was too strong, causing the FID and SD to become right-skewed. The FID and SD of the white ibis was then square-root transformed as this is a less strong transformation than \log_{10} . Visual inspection confirmed that the square-root transformation was successful in normalising the white ibis FID and SD distribution. The \log_{10} - and square-root (sqrt)-transformed values were used in all analyses except for calculating the phi index (Φ), because it is a distribution-free metric (Samia & Blumstein 2014).

An information-theoretic approach was used following the methods suggested by Anderson et al. (2001) to determine the relative importance of year and disturbance level on FID. The general linear models (GLMs) were fitted with a Gaussian error distribution as the transformed FID SD had a normal distribution. The *a priori* model set for variation in FID included all single-to three-factor additive model combinations. Candidate models used additive univariate and multivariate combinations of year and disturbance level. SD was included as a covariate in all the models as SD was not consistent in approaches both within or between years and is known to often correlate with FID in birds (Blumstein 2003). As I had hypothesised that FID would vary between the two years at sites with different levels of disturbance, I included two- and three-factor interactions between the covariate and year and disturbance level.

A similar *a priori* model was used to determine the proportion of birds that walked away in response to the approach by the walker. The logistic regression model was fitted using a GLM with a binomial error structure. The walked response was recorded as 0 or 1, where a value of 0 indicates that a bird flew away and a value of 1 that a bird walked away. The *a priori* model set for variation in the walked response included all single-to three-factor additive model combinations. Candidate models used additive univariate and multivariate combinations of year and disturbance level and square-root/log₁₀FID was included as a covariate. As I had hypothesised that a greater proportion of birds walking away would vary between the two years at sites with different levels of disturbance, I included two- and three-factor interactions between the covariate and year and disturbance level.

Candidate models were selected using Akaike's Information Criterion corrected for small sample sizes (AIC_c) as the number of observations was less than 40 times the number of explanatory variables (Anderson et al. 2001), delta AIC_c (ΔAIC_c), AIC_c weights (w_i) and maximized log-likelihood of the candidate model (Log(L)). Models with the lowest AIC_c and a $\Delta AIC_c < 2$ were considered the most supported candidate models (Burnham & Anderson 2001). Model selection was done using the model.sel function in the MuMIn package in R, which calculates the AIC_c, ΔAIC_c , w_i and Log(L) for each candidate model and orders these models according to their AIC_c (Barton 2018). The percent deviance from the null model that was explained by each of the candidate models was calculated by subtracting the deviance of each null and candidate model and dividing this number by the null model's deviance. The post-hoc Tukey contrasts was used to determine if there were any statistically significant differences in FID and response intensity between the two periods and/or the different disturbance levels between the two periods.

To compare the AD-FID relationship in each of the two periods, I calculated the phi index (Φ) with 10,000 iterations for each species overall and each species at every site disturbance level (Samia & Blumstein 2014). The Φ function evaluates the goodness of the 1:1 relationship between AD and FID (the Φ -value hereafter ‘AD- Φ ’) with Φ -values ranging between 0 and 1. The null expectation is 0.5, where Φ -values > 0.5 indicate an earlier flight and Φ -values < 0.5 a delayed flight (Samia & Blumstein 2014). To compare the AD- Φ between the two periods for each species and site disturbance level, I calculated the 95% confidence interval (CI) using an amended version of the Φ function (D. S. M. Samia pers. comm.). AD- Φ were considered statistically different if the confidence interval did not overlap with the counterpart Φ -value in the other year.

Untransformed FID values are presented in median metres (m) with the lower quartile (Q1) and upper quartile (Q3) range and AD- Φ with CI. Statistical significance for all tests was set at $p < 0.05$. All data analyses were done in R version 3.5.1 (R Core Team 2018).

Results

A total of 255 observations were collected in 2018 during an average of 30 visits per site (range = 30-32), with most observations being for silver gulls (150 observations). This was less than the number of observations collected in 2000 ($n = 726$, 67 site visits (range = 60-89)) (Blumstein et al. 2003). As with the 2000 study, species were not found in equal numbers at each site (Table 3). Only four of the species (white ibis, masked lapwing, pied oystercatcher and silver gull) had sufficient sample sizes in both years and became the focus of this study (see Supplementary Data for summaries on the other species).

Table 3. Number of observations collected for each species, by site disturbance level in 2000 and 2018. Species in bold became the focus of this study as they had the largest sample sizes across both years

	Low		Moderate		High	
	2000	2018	2000	2018	2000	2018
Australian pelican	4	1	8	2	36	0
Australian white ibis	5	3	36	10	20	21
bar-tailed godwit	23	2	22	3	132	3
crested tern	0	0	2	3	59	8
masked lapwing	13	6	5	10	16	3
pied oystercatcher	5	13	15	5	14	3
silver gull	14	5	33	11	225	134
white-faced heron	15	4	15	1	9	4

FID and response intensity

Responses to increasing urbanisation varied between species and site disturbance levels. The information-theoretic GLM analyses showed that the most supported candidate models for each species ($\Delta AIC_c < 2$) included year and the interaction between year and disturbance level for masked lapwing and silver gull FID, and silver gull response intensity (Table 4). There was less than 2 AIC_c between each of the most supported models in each candidate set, indicating the models were all similarly supported.

The most supported candidate models for the white ibis and the pied oystercatcher included year. For the white ibis, year was in the most supported model in the candidate set (Table 4a), with this model explaining 27% of the null model's deviance. White ibis median FID was 11.3 m less in 2018 than in 2000 (2000: 32.2 m (19.6-46.2), 2018: 20.9 m (16.0-30.4)) (Table 5), and this difference was close to significant when using the most supported model in the candidate set (Tukey contrasts: estimate = -0.661, standard error (se) = 0.338, z value = -1.953, $p = 0.051$). However, the difference in FID become significant when the second most supported model (which explains 23% of the null model's deviance) in the candidate set was used (Tukey contrasts: estimate = -0.689, standard error (se) = 0.331, z value = -2.082, $p = 0.037$). For the pied oystercatcher, year was in the second most supported model in the candidate set and the most supported model in this set was also the most parsimonious model (Table 4b). These two models explained about 11% of

the null model's deviance. Although pied oystercatcher median FID was 3.3 m more in 2018 than in 2000 (2000: 34.7 (26.8-46.2); 2018: 37.9 (31.6-45.0)) (Table 5), this difference is not statistically significant (Tukey contrasts: estimate = 0.031, se = 0.051, z value = 0.608, p = 0.543).

The most supported candidate models for the masked lapwing and silver gull FID included the interaction of disturbance level and year and year also for silver gull FID. For the masked lapwing, the interaction term was in the most supported model in the candidate set (Table 4b), with this model explaining 50% of the null model's deviance. While in 2018 the masked lapwing median FID was 16.2 m more at the low disturbance site, 10.1 m more at the moderate disturbance site and 19.4 m less at the high disturbance site (Table 5) than in 2000, none of these differences were statistically significant (Tukey contrasts: $p \geq 0.180$). For the silver gull, the interaction term was also in most supported model in the candidate set (Table 4d), with this model explaining 18% of the null model's deviance. However, the differences in FID were statistically significant at the highly disturbed sites only, with FID 5.1 m less in 2018 than 2000 (Table 5, Figure 2) (Tukey contrasts: estimate = -0.177, se = 0.029, z value = -6.034, $p < 0.001$). Year was in the second most supported model in the candidate set which explained 17% of the null model's deviance. Silver gull FID was also 4.8 m less in 2018 than in 2000 which was statistically significant (Tukey contrasts: estimate = -0.157, se = 0.028, z value = -5.675, $p < 0.001$).

For response intensity, the most supported candidate model included FID, year, disturbance level and the three-factor interaction of disturbance level, FID and year (Table 4e), with this model explaining 8% of the null model's deviance. Fewer birds walked away in 2018 than in 2000, but this was not statistically significant (Tukey contrasts: estimate = -0.291, se = 0.261, z value = -1.114, $p = 0.265$).

Table 4. Most supported candidate models for each species' FID in response to SD as a covariate, disturbance level (low, medium and high) and year (2000 and 2018) and the interactions of SD, disturbance level and year and most supported model for silver gull response intensity in response to FID as a covariate, disturbance level and year. Included are the maximized log-likelihood of the candidate model (Log(L)), Akaike's information criterion (AIC_c), the AIC differences ($\Delta AIC_c = (AIC_c - \min(AIC_c))$), and the rounded Akaike weights (w_i) of each candidate model and the number of estimated parameters for the model (k)

Factor	Candidate model	Log(L)	AIC_c	ΔAIC_c	w_i	k
a) white ibis FID	sqrtSD + disturbancelevel + year	-170.91	354.78	0.000	0.313	5
	sqrtSD + year	-173.27	354.98	0.202	0.283	3
	sqrtSD + sqrtSD:year	-173.88	356.21	1.433	0.153	3
	sqrtSD + disturbancelevel	-172.88	356.44	1.664	0.136	4
	sqrtSD + disturbancelevel:sqrtSD	-173.04	356.76	1.976	0.116	4
b) masked lapwing FID	log ₁₀ SD + disturbancelevel:year	19.84	-20.42	0.000	0.501	8
	log ₁₀ SD + disturbancelevel:log ₁₀ SD	15.32	-19.35	1.062	0.295	4
	log ₁₀ SD + disturbancelevel	14.95	-18.61	1.802	0.204	4
c) pied oystercatcher FID	log ₁₀ SD	16.58	-26.69	0.000	0.569	2
	log ₁₀ SD + year	16.78	-24.75	1.940	0.216	3
	log ₁₀ SD + log ₁₀ SD:year	16.77	-24.74	1.952	0.215	4
d) silver gull FID	log ₁₀ SD + disturbancelevel:year	-39.33	95.02	0.000	0.676	8
	log ₁₀ SD + disturbancelevel+year	-42.14	96.49	1.472	0.324	5
e) silver gull response intensity (walked)	log ₁₀ FID + year + disturbancelevel + disturbancelevel:log ₁₀ FID:year	-178.96	378.57	0.000	1.000	11

Table 5. Median (untransformed) FID with lower quartile (Q1) and upper quartile (Q3) range by species, site disturbance level and year for the four focus species. Blanks indicate no observations collected. See Supplementary data for table with all eight species

Species	low				moderate				high				all			
	2000		2018		2000		2018		2000		2018		2000		2018	
	median	Q1-Q3	median	Q1-Q3	median	Q1-Q3	median	Q1-Q3	median	Q1-Q3	median	Q1-Q3	median	Q1-Q3	median	Q1-Q3
Australian white ibis	31.5	28.0-51.8	33.2	27.8-45.2	32.2	19.3-46.4	28.6	21.7-30.5	31.3	20.3-42.0	17.9	11.7-23.3	32.2	19.6-46.2	20.9	16.0-30.4
masked lapwing	65.8	50.4-82.6	82.0	59.5-93.6	28.0	16.0-72.1	38.1	34.2-39.8	36.4	32.7-43.2	18.7	17.4-22.8	46.2	34.5-66.3	39.4	30.4-54.5
pied oystercatcher	35.0	27.3-53.2	40.4	31.6-46.2	34.3	27.7-47.6	34.8	26.5-37.9	33.3	26.8-38.9	38.0	36.7-50.9	34.7	26.8-46.2	37.9	31.6-45.0
silver gull	23.8	16.3-46.2	42.7	10.5-17.5	14.0	9.8-18.9	14.0	23.0-51.7	14.0	9.5-15.8	8.9	5.60-15.4	14.7	10.2-18.9	9.9	5.7-16.0

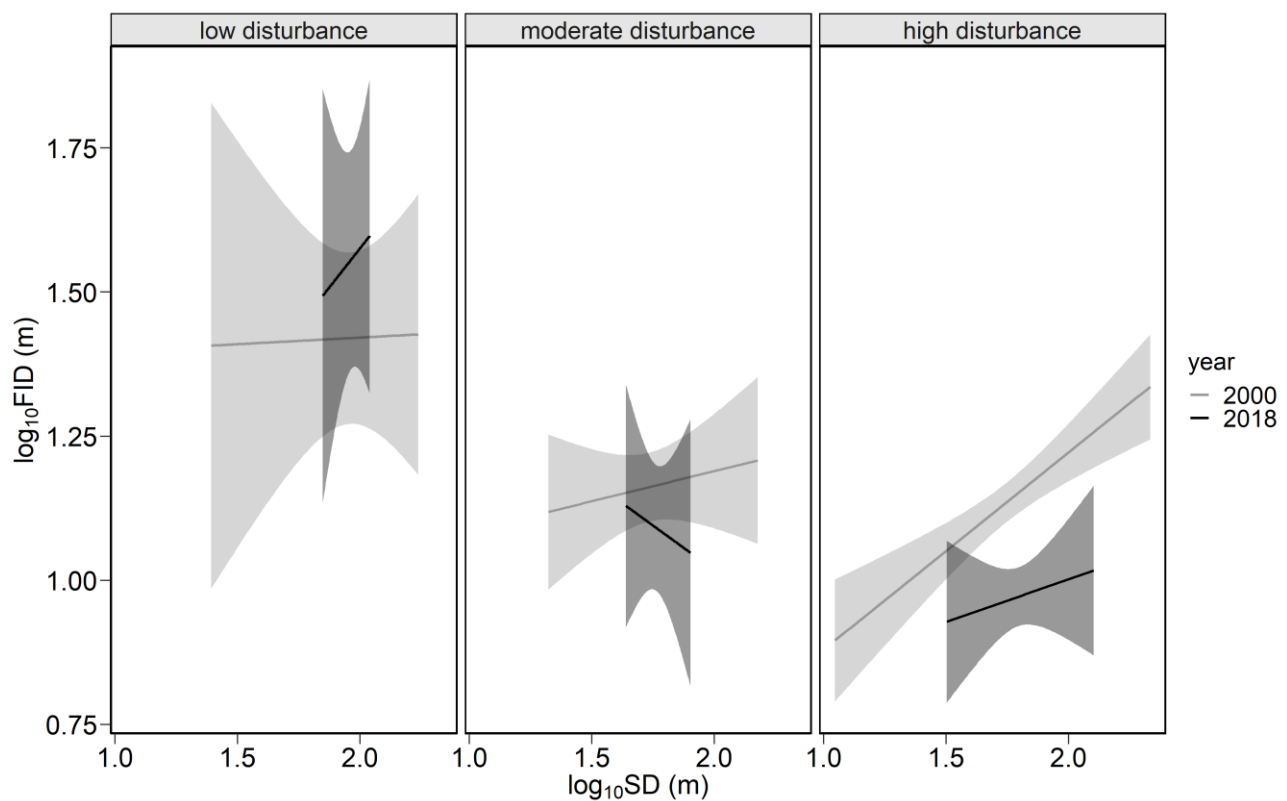


Figure 2. The effect of year and site disturbance level on the relationship between SD and FID for silver gulls. Graph plots $\log_{10}\text{FID}$ by $\log_{10}\text{SD}$ with 95% confidence intervals by site disturbance level and year

Flight initiation after alerting to walker

Comparisons of the AD-FID relationship in the two periods revealed variable responses to urbanisation between species. The white ibis and the silver gull were found to delay flight more in 2018 than in 2000 (Figure 2). For the white ibis, this was at the year level (AD- Φ (CI); 2000: 0.68 (0.58-0.77), 2018: 0.52 (0.44-0.60)) and for the silver gulls, at the year level (2000: 0.49 (0.45-0.54), 2018: 0.40 (0.33-0.48)) and at high disturbance sites (2000: 0.49 (0.44-0.54), 2018: 0.39 (0.31-0.47)). There was no difference in when the masked lapwing initiated flight after detecting the walker at a year level (2000: 0.56 (0.44-0.67), 2018: 0.60 (0.48-0.73)). I had insufficient data to estimate AD- Φ for other species and site disturbance levels.

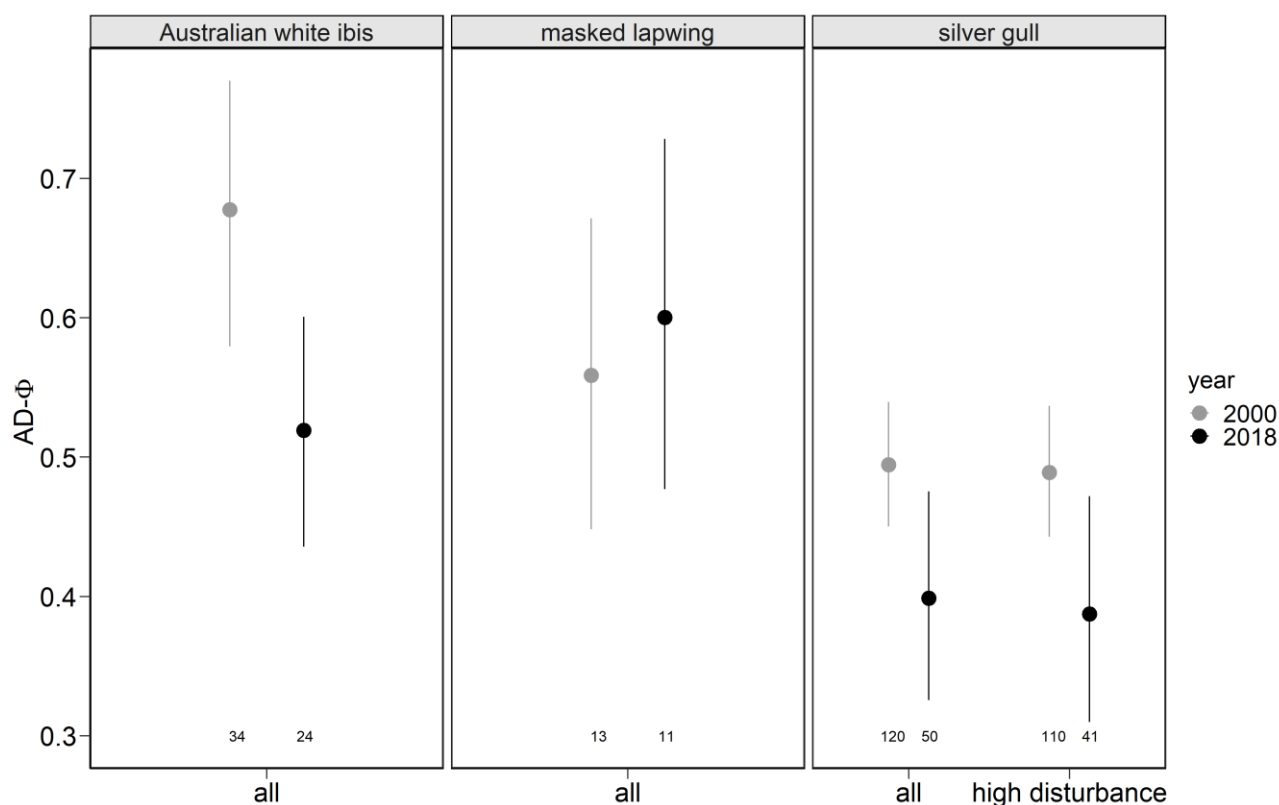


Figure 3. AD-FID relationship in 2000 and 2018 as quantified by the phi index (Φ) for the white ibis, masked lapwing and silver gull for all sites combined and species at each site disturbance level, where $n > 10$ in both 2000 and 2018. Larger AD- Φ values indicate that birds were fleeing earlier and closer to the 1:1 AD-FID relationship than for a lower AD- Φ . Graphs depicts the AD- Φ for each species and site disturbance level with 95% confidence interval and sample size

Discussion

This study investigated urban bird fear responses over two time periods in an area where there has been increasing urbanisation. Fear responses in this study included FID, response intensity (proportion of birds that walked away) and AD-FID relationships. I predicted that species would respond to urbanisation by having a lower FID and response intensity and that AD-FID relationship would be weaker in 2018 than in 2000. I also predicted that any differences found would be greater at the more disturbed sites and for the white ibis, which was one of the more flighty species in the original study. While limited data constrained the comparisons that were able to be made, the white ibis FID was less using the second most supported model and AD-FID was less in 2018 than in 2000. Silver gull FID and the AD-FID relationship were also less in 2018 than 2000 overall, and at

the highly disturbed sites. However, no differences in FID or the AD-FID relationship were detected for the masked lapwing and pied oystercatcher.

As the white ibis and the silver gull are widely considered to be synanthropic species, it was not surprising to see that these two species showed signs of adaptation to increasing urbanisation through decreases in fear responses. The silver gull results of this study are consistent with other studies where lower avian FID has been associated with areas where there are higher levels of human disturbance (e.g. Rollinson & Jones 2006, Díaz et al. 2013). For the silver gulls, the two most supported candidate models explained 17% and 18% of the deviance and for the white ibis the two most supported candidate models explained 27% and 23% of the deviance, respectively. This suggests that there are factors other than year and disturbance level influencing their FID. This agrees with other research which have found that there are several other factors that influence FID (Stankowich & Blumstein 2005), including distance to refuge, sex (Guay et al. 2013) and environmental factors, including cloud cover (Webb & Blumstein 2005) affect FID, although these influences were not assessed in this study.

Both the white ibis and the silver gull delayed initiating flight more in 2018 than in 2000, which is consistent with rural and urban comparisons of the same species (Samia et al. 2017). All species are expected to optimise when they fly as in they need to balance the cost of taking flight against the benefit, and any risks, of staying (Ydenberg & Dill 1986). In urban areas, predation pressures may be reduced due to loss of predators (Møller & Ibáñez-Álamo 2012), although urban cats (Baker et al. 2008) and dogs (Hughes & Macdonald 2013) continue to have impacts on wildlife. Synanthropic species may further benefit from the increased availability of human sourced food, as has been seen for both these species (Smith & Carlile 1993, Martin et al. 2010). In such circumstances, the costs of association with humans may be outweighed by the benefits. While it is unknown what proportion anthropogenic food contributes to the diet of the white ibis and silver gull in this area, it is likely that this surfeit of food has encouraged their increased tolerance to humans.

Greater tolerance to humans may also arise as increasing presence with human populations may allow animals to fine-tune their ability to assess the risk posed by humans (Parker & Nilon 2008). Levels of vigilance have been linked to the perceived level of risk (Frid & Dill 2002, Stankowich & Blumstein 2005) and perceived level of risk has been identified as a factor that can influence the relationship between AD and FID (Tätte et al. 2018). The weaker AD-FID relationships seen in this study are consistent with earlier comparisons between rural and urban birds. In other studies, urban birds have been found to have a weaker AD-FID relationship than rural birds (Samia et al. 2017).

Delaying flight results in animals incurring higher monitoring costs and is not consistent with the FEAR hypothesis, where animals should flee earlier after detecting a potential threat to avoid ongoing monitoring costs (Blumstein 2010). This may be due to a need to balance monitoring costs against the costs of repetitive flight in high human traffic areas, combined with the bird's experience of interacting with humans in an area where disturbance is non-lethal or relatively harmless.

Given the benefits of increased tolerance towards humans in relation to increasing urbanisation, I did not expect that the masked lapwing would show no indication of change in fear responses. Masked lapwings are often found on lawns in private gardens (Daniels & Kirkpatrick 2006) and using artificial structures as nesting sites. Masked lapwings also have higher breeding success and modulate their behaviour in urban compared to non-urban areas (Cardilini et al. 2013). Interactions between humans and this species are known to occur, especially during the breeding season when masked lapwings aggressively defend their young (Lees et al. 2013). These factors demonstrate behavioural flexibility and are all indicators of an *adaptable* species and hence, further increases in tolerance towards humans would be expected. However, in terms of interacting with humans, unlike the silver gulls and the Australian white ibis, which can benefit from both indirect and direct feeding by humans (pers.obs.), masked lapwings appear to indirectly benefit from the built environment. Therefore, there may be less of an advantage in delaying flight, especially when alternative options are available.

The absence of any indicators of change in fear responses of the pied oystercatcher was also unexpected. This species is known to rely on natural resources and there is an association between their distribution on beaches and these food resources (Owner & Rohweder 2003, Meager et al. 2012). Although pied oystercatchers also rest on anthropogenic structures such as wooden pylons and rock walls (pers. obs.), their reliance on natural resources indicates that it is possible that this is an *avoider* species, which is associated with lower behavioural flexibility. However, I would be hesitant to draw any firm conclusions from the masked lapwing and pied oystercatcher results due to the small sample sizes. It is also possible that the pied oystercatcher and masked lapwing did not show any signs of further adjustments to increasing urbanisation as their fear responses in 2000 were still suitable for them in 2018.

The results of this study suggest heterogeneous behavioural responses to increasing urbanisation. Variability in fear responses between species in relation to exposure to humans is expected, given studies on shorebirds within a single time period (Glover et al. 2011, Schlacher et al. 2013). I

predicted intraspecific differences between the two periods and that this would occur more at the highly disturbed sites and for the white ibis. While year had an effect on the FID of all four species, the interaction of year and disturbance level only had an effect on the masked lapwing and silver gull. The white ibis FID results in particular did not match my expectations, with one model indicating a marginally non-significant result and another a significant decrease in FID. This was unexpected as this species has undergone recent population growth in the Sydney area and has a reputation for scavenging human-sourced food (Martin et al. 2010), which are hallmarks of an exploiter species. Admittedly, there were small sample sizes overall, especially at the moderate and low disturbance sites for each of the four species, which could have contributed to this result. Variation in responses to increasing urbanisation may also be due to some species, and even individuals, adapting in different ways. Additional research is required to better assess variation in responses and how these can vary over short and long time periods and at different spatial scales (sensu Fleming & Bateman 2017). Group size, while not analysed in this study, has been found to affect AD, but not FID (e.g. Guay et al. 2013, Fleming & Bateman 2017, Mikula et al. 2018), although this can vary between taxa (Stankowich & Blumstein 2005).

At present, it is not fully understood how variation or consistency in behavioural fear responses of different species can arise within an area during different time periods. Three mechanisms that have been proposed to explain variation in avian fear responses in areas of different levels of human disturbance within a single time period are particularly pertinent to this study (see Webb & Blumstein 2005). First, individuals may have relatively consistent fear responses throughout their lifetimes, as have been found in burrowing owls (Carrete & Tella 2010), or they adjust their behaviours over time, possibly due to learning (Van Donselaar et al. 2018). Second, individuals may adjust their behaviour at different sites in response to differing levels of human disturbance, as has been found for silver gulls (Fleming & Bateman 2017) and western gulls (Webb & Blumstein 2005). Thirdly, individuals may distribute themselves according to their fear responses, with individuals that are highly tolerant persisting in areas of higher disturbance and birds that are less tolerant avoiding such areas (Carrete & Tella 2011). Banding records show that the silver gull, masked lapwing and pied oystercatcher can live for more than 18 years (Australian Bird and Bat Banding Scheme 2018), and so it is possible that some of these birds could have been alive at the time of the original study in 2000. In this study, the sites were all within a short distance of each other and so it is possible that individuals have moved between the sites or left the area entirely. While assessing the influence of these mechanisms on fear responses was out of the scope for this project, future studies could band, track and assess fear responses of individuals from different species over time. This may help explain why some species show variation in behaviour in relation

to human disturbance levels while other species do not. Such research would also increase understanding of the links between individual behaviour and species-level responses in areas of increasing urbanisation.

Understanding how increasing urbanisation may affect avian fear responses in different time periods is an important part of improving the understanding of anti-predatory behaviour. In this study, I have shown that the white ibis and especially the silver gull appear to be responding to increasing urbanisation by further increasing their tolerance to humans, although year had an effect on all four species' FID. Other species, especially those not considered to be synanthropic species, do not appear to be responding in the same way. This has implications for understanding how anti-predatory behaviour can change as a response to increasing urbanisation in Sydney, Australia and around the world. Although this study has only compared two time periods, the results are consistent with findings of other studies in relation to increasing urbanisation along a rural-urban gradient and over time. Future studies could expand upon this work by repeating this study with greater sample sizes to investigate whether there are any trends in the fear responses of these species and examining the responses of other urban animals over time in relation to increasing urbanisation. This will improve the understanding of FID in the context of the situations in which these species encounter potential threats, and how some species may benefit more from delaying flight than others.

Acknowledgements

Research was conducted under animal use protocols approved by Macquarie University Animal Ethics Committee (# 2018/005) and a scientific licence issued by the New South Wales National Parks and Wildlife Service (# SL102057). Permission to undertake research at Penrhyn Foreshore was kindly granted by the Port Authority of New South Wales. I thank Laura Anthony for collection of the 2000 data and Andrew Allen for his statistical advice. I was supported by an Australian Government Research Training Program Scholarship and Benjamin Pitcher was partially funded by a Macquarie University Research Fellowship.

References

- Agardy T, Bridgewater P, Crosby MP, Day J, Dayton PK, Kenchington R, Laffoley D, McConney P, Murray PA, Parks JE (2003) Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13:353-367
- Anderson DR, Link WA, Johnson DH, Burnham KP (2001) Suggestions for presenting the results of data analyses. *The Journal of Wildlife Management* 65:373-378
- Andrzejewski R, Babińska-Werka J, Gliwicz J, Goszczyński J (1978) Synurbanization processes in population of *Apodemus agrarius*. I. Characteristics of populations in an urbanization gradient. *Acta theriologica* 23:341-358
- Aronson MFJ, Sorte FAL, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS, Williams NSG, Cilliers S, Clarkson B, Dobbs C, Dolan R, Hedblom M, Klotz S, Kooijmans JL, Kühn I, MacGregor-Fors I, McDonnell M, Mörtberg U, Pyšek P, Siebert S, Sushinsky J, Werner P, Winter M (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences* 281:20133330
- Australian Bird and Bat Banding Scheme (2018) Australian bird and bat banding database, Australian Government Department of the Environment and Energy. Accessed 8 October 2018. <http://www.environment.gov.au/topics/science-and-research/bird-and-bat-banding/banding-data/search-abbbs-database>
- Australian Bureau of Statistics (2018) Media Release- What's driving population growth in Australia's cities? Accessed 3 September 2018. <http://www.abs.gov.au/ausstats/abs@.nsf/Latestproducts/3218.0Media%20Release12016-17?opendocument&tabname=Summary&prodno=3218%E2%80%A6>
- Baker PJ, Molony SE, Stone E, Cuthill IC, Harris S (2008) Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? *Ibis* 150:86-99
- Banaszak-Cibicka W, Żmihorski M (2012) Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation* 16:331-343
- Barton K (2018) MuMIn: Multi-Model Inference. <https://CRAN.R-project.org/package=MuMIn>
- Bateman PW, Fleming PA (2012) Big city life: carnivores in urban environments. *Journal of Zoology* 287:1-23
- Battles AC, Moniz M, Kolbe JJ (2018) Living in the big city: preference for broad substrates results in niche expansion for urban *Anolis* lizards. *Urban Ecosystems* 21:1087–1095
- Baxter AT, Allan JR (2008) Use of lethal control to reduce habituation to blank rounds by scavenging birds. *Journal of Wildlife Management* 72:1653-1657
- Bejder L, Samuels A, Whitehead H, Finn H, Allen S (2009) Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series* 395:177-185
- Blair RB (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications* 6:506-519
- Blair RB (2001) Birds and butterflies along urban gradients in two ecoregions of the US In: Lockwood JL, McKinney ML (eds) *Biotic homogenization*. Kluwer, Norwell
- Blair RB, Launer AE (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. *Biological Conservation* 80:113-125
- Blumstein DT (2003) Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management* 67:852-857
- Blumstein DT (2006) Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour Forum* 71:389-399
- Blumstein DT (2010) Flush early and avoid the rush: a general rule of antipredator behavior? *Behavioral Ecology* 21:440-442
- Blumstein DT (2016) Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour* 120:255-262

- Blumstein DT, Anthony LL, Harcourt R, Ross G (2003) Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation* 110:97-100
- Bonenfant M, Kramer DL (1996) The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behavioral Ecology* 7:299-303
- Bradley CA, Altizer S (2007) Urbanization and the ecology of wildlife diseases. *Trends in Ecology & Evolution* 22:95-102
- Burnham KP, Anderson DR (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28:111-119
- Cardilini APA, Weston MA, Nimmo DG, Dann P, Sherman CDH (2013) Surviving in sprawling suburbs: suburban environments represent high quality breeding habitat for a widespread shorebird. *Landscape and Urban Planning* 115:72-80
- Cardno (2018) Port Botany Post Construction Environmental Monitoring Annual Report 2016. Prepared for Port Authority of NSW, 20 February 2018.
- Carney KM, Sydeman WJ (1999) A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22:68-79
- Carpenter LH, Decker DJ, Lipscomb JF (2000) Stakeholder acceptance capacity in wildlife management. *Human Dimensions of Wildlife* 5:5-19
- Carrete M, Tella JL (2010) Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biology Letters* 6:167-170
- Carrete M, Tella JL (2011) Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS ONE* 6:e18859
- Chamaillé-Jammes S, Blumstein DT (2012) A case for quantile regression in behavioral ecology: getting more out of flight initiation distance data. *Behavioral Ecology and Sociobiology* 66:985-992
- Chan AAY-H, Giraldo-Perez P, Smith S, Blumstein DT (2010) Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters* 6:458-461
- Clucas B, Marzluff JM, Kübler S, Meffert P (2011) New directions in urban avian ecology: reciprocal connections between birds and humans in cities. In: Endlicher W, Hostert P, Kowarik I, Kulke E, Lossau J, Marzluff J, Meer E, Mieg H, Nützmann G, Schulz M, Wessolek G (eds) *Perspectives in urban ecology: Studies of ecosystems and interactions between humans and nature in the metropolis of Berlin*. Springer, Berlin, Germany
- Cooke A (1980) Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biological Conservation* 18:85-88
- Cooper Jr WE, Attum O, Kingsbury B (2008) Escape behaviors and flight initiation distance in the common water snake *Nerodia sipedon*. *Journal of Herpetology* 42:493-500
- Cooper Jr WE, Blumstein DT (2015) *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge, United Kingdom
- Daniels G, Kirkpatrick J (2006) Does variation in garden characteristics influence the conservation of birds in suburbia? *Biological Conservation* 133:326-335
- Department of Infrastructure, Regional Development and Cities (2018) Monthly airport traffic data for top twenty airports: January 2009 to current. Accessed 16 August 2018. https://bitre.gov.au/publications/ongoing/airport_traffic_data.aspx
- DeStefano S, DeGraaf RM (2003) Exploring the ecology of suburban wildlife. *Frontiers in Ecology and the Environment* 1:95-101
- Díaz M, Møller AP, Flensted-Jensen E, Grim T, Ibáñez-Álamo JD, Jokimäki J, Markó G, Tryjanowski P (2013) The geography of fear: a latitudinal gradient in anti-predator escape. *PLoS ONE* 8:e64634
- Dill LM, Houtman R (1989) The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Canadian Journal of Zoology* 67:233-235

- Donnelly R, Marzluff J (2004) Designing research to advance the management of birds in urbanizing areas. In: Shaw WW, Harris LK, Vandruff L (eds). Proceedings of the 4th International Symposium on Urban Wildlife Conservation
- Fernández-Juricic E (2000) Local and regional effects of pedestrians on forest birds in a fragmented landscape. *The Condor* 102:247-255
- Fernández-Juricic E, Jimenez M, Lucas E (2002) Factors affecting intra-and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology* 80:1212-1220
- Fernández-Juricic E, Tellería JL (2000) Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study* 47:13-21
- Fernández-Juricic E, Venier MP, Renison D, Blumstein DT (2005) Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biological Conservation* 125:225-235
- Fidino M, Magle SB (2017) Trends in long-term urban bird research. In: Murgui E, Hedblom M (eds) *Ecology and Conservation of Birds in Urban Environments*. Springer, Cham, Switzerland
- Fischer JD, Cleeton SH, Lyons TP, Miller JR (2012) Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *Bioscience* 62:809-818
- Fleming PA, Bateman PW (2017) Scavenging opportunities modulate escape responses over a small geographic scale. *Ethology* 123:205-212
- Francis RA, Chadwick MA (2012) What makes a species synurbic? *Applied Geography* 32:514-521
- Frid A, Dill L (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11-26
- Garcia CM, Suárez-Rodríguez M, López-Rull I (2017) Becoming citizens: avian adaptations to urban life. In: Murgui E, Hedblom M (eds) *Ecology and Conservation of Birds in Urban Environments*. Springer International Publishing, Cham, Switzerland
- Giese M (1998) Guidelines for people approaching breeding groups of Adélie penguins (*Pygoscelis adeliae*). *Polar Record* 34:287-292
- Glover HK, Weston MA, Maguire GS, Miller KK, Christie BA (2011) Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. *Landscape and Urban Planning* 103:326-334
- Groves PM, Thompson RF (1970) Habituation: a dual-process theory. *Psychological Review* 77:419-450
- Guay P-J, Lorenz RD, Robinson RW, Symonds MR, Weston MA (2013) Distance from water, sex and approach direction influence flight distances among habituated black swans. *Ethology* 119:552-558
- Guay P-J, van Dongen WFD, Robinson RW, Blumstein DT, Weston MA (2016) AvianBuffer: An interactive tool for characterising and managing wildlife fear responses. *Ambio* 45:841-851
- Hughes J, Macdonald DWJBC (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation* 157:341-351
- Infrastructure Australia (2018) *Future Cities: Planning for our growing population*.
- Jack KM, Lenz BB, Healan E, Rudman S, Schoof VAM, Fedigan L (2008) The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. *American Journal of Primatology* 70:490-494
- Johns BG (1996) Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. *Biological Conservation* 78:257-262
- Kekkonen J (2017) Pollutants in urbanized areas: direct and indirect effects on bird populations. In: Murgui E, Hedblom M (eds) *Ecology and Conservation of Birds in Urban Environments*. Springer, Cham, Switzerland

- Kochert MN, Collopy MW (1998) Relevance of research to resource managers and policy makers. In: Marzluff JM, Sallabanks R (eds) *Avian Conservation: Research and Management*. Island Press, Washington DC, USA
- Layne Jr JR, Ford NB (1984) Flight distance of the queen snake, *Regina septemvittata*. *Journal of Herpetology* 18:496-498
- Lee PF, Ding TS, Hsu FH, Geng S (2004) Breeding bird species richness in Taiwan: distribution on gradients of elevation, primary productivity and urbanization. *Journal of Biogeography* 31:307-314
- Lees D, Sherman C, Maguire G, Dann P, Cardilini A, Weston M (2013) Swooping in the suburbs; parental defence of an abundant aggressive urban bird against humans. *Animals* 3:754-766
- Lepczyk CA, La Sorte FA, Aronson MFJ, Goddard MA, MacGregor-Fors I, Nilon CH, Warren PS (2017) Global patterns and drivers of urban bird diversity. In: Murgui E, Hedblom M (eds) *Ecology and Conservation of Birds in Urban Environments*. Springer, Cham, Switzerland
- Lowry H, Lill A, Wong BBM (2013) Behavioural responses of wildlife to urban environments. *Biological Reviews* 88:537-549
- Luck GW (2007) A review of the relationships between human population density and biodiversity. *Biological Reviews* 82:607-645
- Luniak M (2004) Synurbization—adaptation of animal wildlife to urban development. In: Shaw WW, Harris LK, Vandruff L (eds). *Proceedings of the 4th International Symposium on Urban Wildlife Conservation*
- Madden F (2004) Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Human Dimensions of Wildlife* 9:247-257
- Magle SB, Hunt VM, Vernon M, Crooks KR (2012) Urban wildlife research: past, present, and future. *Biological Conservation* 155:23-32
- Martin J, French K, Major R (2010) Population and breeding trends of an urban coloniser: the Australian white ibis. *Wildlife Research* 37:230-239
- Martin JM, French K, Major RE (2007) The pest status of Australian white ibis (*Threskiornis molucca*) in urban situations and the effectiveness of egg-oil in reproductive control. *Wildlife Research* 34:319-324
- Marzluff JM, Bowman R, Donnelly R (2001) A historical perspective on urban bird research: trends, terms, and approaches. In: Marzluff JM, Bowman R, Donnelly R (eds) *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publishers, Boston, USA
- McIntyre NE, Knowles-Yáñez K, Hope D (2000) Urban ecology as an interdisciplinary field: differences in the use of “urban” between the social and natural sciences. *Urban Ecosystems* 4:5-24
- McKinney M (2002) Urbanization, biodiversity, and conservation. *BioScience* 52:883–890
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247-260
- Meager JJ, Schlacher TA, Nielsen T (2012) Humans alter habitat selection of birds on ocean-exposed sandy beaches. *Diversity and Distributions* 18:294-306
- Ménard N, Foulquier A, Vallet D, Qarro M, Le Gouar P, Pierre JS (2014) How tourism and pastoralism influence population demographic changes in a threatened large mammal species. *Animal Conservation* 17:115-124
- Mikula P, Díaz M, Møller AP, Albrecht T, Tryjanowski P, Hromada M (2018) Migratory and resident waders differ in risk taking on the wintering grounds. *Behavioural Processes* 157:309-314
- Miranda AC (2017) Mechanisms of behavioural change in urban animals: the role of microevolution and phenotypic plasticity. In: Murgui E, Hedblom M (eds) *Ecology and Conservation of Birds in Urban Environments*. Springer International Publishing Cham, Switzerland

- Møller AP (2009) Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* 159:849-858
- Møller AP (2010) Interspecific variation in fear responses predicts urbanization in birds. *Behavioral Ecology* 21:365-371
- Møller AP, Ibáñez-Álamo JD (2012) Escape behaviour of birds provides evidence of predation being involved in urbanization. *Animal Behaviour* 84:341-348
- Niemelä J (1999) Is there a need for a theory of urban ecology? *Urban Ecosystems* 3:57-65
- Nisbet ICT (2000) Disturbance, habituation, and management of waterbird colonies. *Waterbirds* 23:312-332
- Office of Environment and Heritage (2011) The shorebird community occurring on the relict tidal delta sands at Taren Point - endangered ecological community listing. Accessed 7 June 2018.
<https://www.environment.nsw.gov.au/determinations/ShorebirdCommunityTarenPointEndComListing.htm>
- Owner D, Rohweder D (2003) Distribution and habitat of Pied Oystercatchers (*Haematopus longirostris*) inhabiting ocean beaches in northern New South Wales. *Emu* 103:163-169
- Ozel LD, Stynoski JL (2011) Differences in escape behavior between a cryptic and an aposematic litter frog. *Journal of Herpetology* 45:395-398
- Parker TS, Nilon CH (2008) Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosystems* 11:243-255
- Pauleit S, Ennos R, Golding Y (2005) Modeling the environmental impacts of urban land use and land cover change-a study in Merseyside, UK. *Landscape and Urban Planning* 71:295-310
- Pichegru L, Edwards TB, Dilley BJ, Flower TP, Ryan PG (2016) African penguin tolerance to humans depends on historical exposure at colony level. *Bird Conservation International* 26:307-322
- Piratelli AJ, Favoretto GR, de Almeida Maximiano MF (2015) Factors affecting escape distance in birds. *Zoologia* 32:438-444
- Pomeroy RS, Watson LM, Parks JE, Cid GA (2005) How is your MPA doing? A methodology for evaluating the management effectiveness of marine protected areas. *Ocean and Coastal Management* 48:485-502
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria
- Rankin CH, Abrams T, Barry RJ, Bhatnagar S, Clayton DF, Colombo J, Coppola G, Geyer MA, Glanzman DL, Marsland S, McSweeney FK, Wilson DA, Wum C-F, Thompson RF (2009) Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory* 92:135-138
- Rebele F (1994) Urban ecology and special features of urban ecosystems. *Global Ecology and Biogeography Letters* 4:173-187
- Rhoades OK, Lonhart SI, Stachowicz JJ (2018) Fished species uniformly reduced escape behaviors in response to protection. *Biological Conservation* 226:238-246
- Riley SP, Hadidian J, Manski DA (1998) Population density, survival, and rabies in raccoons in an urban national park. *Canadian Journal of Zoology* 76:1153-1164
- Rodríguez-Prieto I, Fernández-Juricic E (2005) Effects of direct human disturbance on the endemic Iberian frog *Rana iberica* at individual and population levels. *Biological Conservation* 123:1-9
- Rollinson DJ, Jones DN (2006) Tolerance of Australian magpies *Gymnorhina tibicen* towards humans: A comparison along an urban gradient. *Australian Field Ornithology* 23:29-35
- Roux DJ, Rogers KH, Biggs HC, Ashton PJ, Sergeant A (2006) Bridging the science–management divide: moving from unidirectional knowledge transfer to knowledge interfacing and sharing. *Ecology and Society* 11:4
- Runyan AM, Blumstein DT (2004) Do individual differences influence flight initiation distance? *Journal of Wildlife Management* 68:1124-1129

- Samia DSM, Blumstein DT (2014) Phi index: a new metric to test the flush early and avoid the rush hypothesis. *PLoS ONE* 9:e113134
- Samia DSM, Blumstein DT, Díaz M, Grim T, Ibáñez-Álamo JD, Jokimäki J, Tätté K, Markó G, Tryjanowski P, Møller AP (2017) Rural-urban differences in escape behavior of European birds across a latitudinal gradient. *Frontiers in Ecology and Evolution* 5:66
- Samia DSM, Nomura F, Blumstein DT (2013) Do animals generally flush early and avoid the rush? A meta-analysis. *Biology Letters* 9:20130016
- Sbragaglia V, Morroni L, Bramanti L, Weitzmann B, Arlinghaus R, Azzurro E (2018) Spearfishing modulates flight initiation distance of fishes: the effects of protection, individual size, and bearing a speargun. *ICES Journal of Marine Science* 75:1779-1789
- Schlacher TA, Nielsen T, Weston MA (2013) Human recreation alters behaviour profiles of non-breeding birds on open-coast sandy shores. *Estuarine, Coastal and Shelf Science* 118:31-42
- Seto KC, Fragkias M, Güneralp B, Reilly MK (2011) A meta-analysis of global urban land expansion. *PLoS ONE* 6:e23777
- Shanahan DF, Strohbach MW, Warren PS, Fuller RA (2014) The challenges of urban living. In: Gil D, Brumm H (eds) *Avian Urban Ecology Behavioural and Physiological Adaptations*. Oxford University Press, Oxford, United Kingdom
- Smith ACM (2009) Population ecology of the Australian white ibis, *Threskiornis molucca*, in the urban environment. Doctor of Philosophy, University of Technology, Sydney,
- Smith GC, Carlile N (1993) Food and feeding ecology of breeding silver gulls (*Larus novaehollandiae*) in urban Australia. *Colonial waterbirds* 16:9-16
- Sol D, González-Lagos C, Lapiedra O, Díaz M (2017) Why are exotic birds so successful in urbanized environments? In: Murgui E, Hedblom M (eds) *Ecology and Conservation of Birds in Urban Environments*. Springer, Cham, Switzerland
- Stankowich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London B: Biological Sciences* 272:2627-2634
- Tätté K, Møller AP, Mänd R (2018) Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled. *Animal Behaviour* 136:75-86
- Timm RM, Baker RO, Bennett JR, Coolahan CC (2004) Coyote attacks: an increasing suburban problem. In: Timm RM, Gorenzel WP (eds). *Proceedings of the North American Wildlife and Natural Resources Conference*
- United Nations, Department of Economic and Social Affairs, Population Division (2014) *World Urbanization Prospects: The 2014 Revision, Highlights*. (ST/ESA/SERA/352)
- United Nations, Department of Economic and Social Affairs, Population Division (2017) *World Population Prospects: The 2017 Revision, Key Findings and Advance Tables*. Working Paper No ESA/P/WP/248
- Van Dongen WF, McLeod EM, Mulder RA, Weston MA, Guay P-J (2015) The height of approaching humans does not affect flight-initiation distance. *Bird Study* 62:285-288
- Van Donselaar JL, Atma JL, Kruijff ZA, LaCroix HN, Proppe DS (2018) Urbanization alters fear behavior in black-capped chickadees. *Urban Ecosystems* 21:1043-1051
- Warren P, Tripler C, Bolger D, Faeth S, Huntly N, Lepczyk C, Meyer J, Parker T, Shochat E, Walker J (2006) Urban food webs: predators, prey, and the people who feed them. *Bulletin of the Ecological Society of America* 87:387-393
- Watkins WA (1986) Whale reactions to human activities in Cape Cod waters. *Marine Mammal Science* 2:251-262
- Webb NV, Blumstein DT (2005) Variation in human disturbance differentially affects predation risk assessment in western gulls. *The Condor* 107:178-181
- Weston MA, Elgar MA (2007) Responses of incubating hooded plovers (*Thinornis rubricollis*) to disturbance. *Journal of Coastal Research* 23:569-576
- Weston MA, McLeod EM, Blumstein DT, Guay P-J (2012) A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu* 112:269-286

- Whitfield R (2011) Taren Point Shorebird Reserve. Australasian Parks and Leisure - Summer 2011 14:11-12
- Woodford MH, Butynski TM, Karesh WB (2002) Habituating the great apes: the disease risks. *Oryx* 36:153-160
- Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. *Advances in the Study of Behavior* 16:229-249

Supplementary data

Appendix A: Median FID for all species

Table S1. Median (untransformed) FID with lower quartile (Q1) and upper quartile (Q3) range by species, site disturbance level and year for all eight species. Blanks indicate no observations collected

Species	Low				Moderate				High			
	2000 median	Q1-Q3	2018 median	Q1-Q3	2000 median	Q1-Q3	2018 median	Q1-Q3	2000 median	Q1-Q3	2018 median	Q1-Q3
Australian pelican	66.5	52.2-75.3	85.2	85.2-85.2	30.8	28.0-41.0	38.3	34.7-41.8	22.1	14.8-38.2		
Australian white ibis	31.5	28.0-51.8	33.2	27.8-45.2	32.2	19.3-46.4	28.6	21.7-30.5	31.3	20.3-42.0	17.9	11.7-23.3
bar-tailed godwit	29.4	23.6-44.1	63.9	57.2-70.7	22.1	15.8-31.3	11.2	11.2-12.9	16.5	12.6-22.6	16.2	14.8-26.4
crested tern					39.9	35.4-44.5	16.3	15.2-17.1	14.8	10.5-21.7	12.8	10.9-19.6
masked lapwing	65.8	50.4-82.6	82.0	59.5-93.6	28.0	16.0-72.1	38.1	34.2-39.8	36.4	32.7-43.2	18.7	17.4-22.8
pied oystercatcher	35.0	27.3-53.2	40.4	31.6-46.2	34.3	27.7-47.6	34.8	26.5-37.9	33.3	26.8-38.9	38.0	36.7-50.9
silver gull	23.8	16.3-46.2	42.7	10.5-17.5	14.0	9.8-18.9	14.0	23.0-51.7	14.0	9.5-15.8	8.9	5.60-15.4
white-faced heron	28.0	16.8-46.6	35.4	31.1-39.9	31.5	20.3-36.8	58.2	58.2-58.2	25.9	21.7-40.6	20.1	13.8-23.2



MACQUARIE
University

ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2018/005

Date of Expiry: 18 February 2019

Full Approval Duration: 19 February 2018 to 18 February 2020

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).

Principal Investigator:

Doctor Benjamin Pitcher
Department of Biological Sciences
Macquarie University, NSW 2109
ben.pitcher@mq.edu.au
0468 366 345

Associate Investigators:

Rob Harcourt 0421 780 434
Kathleen Smiley 0422 676 826

In case of emergency, please contact:
the Principal Investigator / Others named above
or **Animal Welfare Officer:** 9850 7758 / 0439 497 383

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project: Flight initiation distance in birds, urbanisation and habituation

Purpose: 4 - Research: Human or Animal Biology

Aims: To examine how different species of shorebirds respond to human disturbance

Surgical Procedures category: 3 - Minor Conscious Intervention

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Maximum numbers approved for the full Approval Duration:

Species	Strain	Age/Weight/Sex	Total	Supplier/Source
20 - Native Wild Birds	silver gull - <i>Larus novaehollandiae</i>	Any	420	Wild/In Situ
	bar-tailed godwit - <i>Limosa lapponica</i>		420	
	crested tern - <i>Sterna bergii</i>		420	
	white ibis - <i>Threskiornis molucca</i>		420	
	Australian pelican - <i>Pelecanus conspicillatus</i>		420	
	white-faced heron - <i>Ardea novaehollandiae</i>		420	
	masked lapwing - <i>Vanellus miles</i>		420	
	pied oystercatcher - <i>Haemtopus longirostris</i>		420	
	Galah - <i>Eolophus roseicapilla</i>		420	
		TOTAL	3780	

Location of research:

Location
Locations around Botany Bay NSW
Macquarie University Campus

Amendments approved by the AEC since initial approval: N/A

Conditions of Approval: N/A

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

A/Prof. Nathan Hart (Chair, Animal Ethics Committee)

Approval Date: 15 February 2018