

Biological, behavioural and life history
traits associated with range expansion of
common mynas (*Acridotheres tristis*) in
Australia

by

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Statements

I hereby certify that the work embodied in this thesis is my own work, conducted under normal supervision.

This thesis contains no material which has been accepted, or is being examined, for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. I give consent to the final version of my thesis being made available worldwide when deposited in the University's Digital Repository, subject to the provisions of the Copyright Act 1968 and any approved embargo.

Candidate signature.....

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What a crazy idea, a PhD at 46 years old. I wanted to submit this thesis for my 50th, but I am still not 51 when I write these lines, so almost! This fascinating and difficult four years' adventure would not have been possible without the wonderful people I have met along the road.

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Abstract

Invasive species have been recognized as the second major threat to biodiversity just following habitat destruction. Biotic invasions science over recent decades has invested substantial research efforts in identifying the factors (e.g., biologic, ecologic, behavioural, genetic) that help predict invasiveness ability in order to anticipate and prevent future invasions. A range of studies have examined the multiple stages in the invasion process from transport to invasion. However, to date, less attention has been given to an important step of the invasion process: spread. In order to enhance the scientific knowledge about invasive species and the patterns and drivers of spread, this thesis aimed to study the common (Indian) myna's (*Acridotheres tristis*) ongoing invasion in Australia with emphasis on NSW and QLD. This case study offers an exceptional opportunity and natural experiment for studying individuals at different stages of the invasion process simultaneously and in real time. I took advantage of this setting to investigate for the first time the potential differences in both morphological and behavioural traits in long-established (>40 years; also termed source) vs recently-established (<10 years; front) common myna populations (Chapters 1 and 2). Furthermore, I studied the interactions of common mynas with native avian species around nesting resources. I focused on interactions with an important cavity-nesting competitor, the eastern rosella (*Platycercus eximius*), and a non-cavity nesting, but highly aggressive, despotic and territorial native honeyeater, the noisy miner (*Manorina melanocephala*) (Chapters 3 and 4). In my final chapter, I undertook a large-scale analysis of common myna abundance and breeding success as a function of habitat and invasion stage across two Australian states (Queensland and New South Wales). I found differences in morphological, physiological and behavioural traits of common mynas at different invasion stages and across regions. On the front of the invasion, common

mynas exhibited longer beaks, better health and a higher level of neophobia. My study of the native vs. invasive bird species revealed that contrary to common believe, common mynas in NSW did not display substantial aggression towards native parrots. In contrast, the native noisy miner exhibited high levels of aggressiveness towards common mynas. Moreover, I discovered that mynas in NSW were more abundant in urban areas than in suburban areas, whereas in QLD, mynas were equally abundant across the two environments. Finally, I found evidence that common mynas first colonise urban habitats during their range expansion. Using my thesis findings, I propose a model whereby common mynas are expanding their distribution across Eastern NSW by moving out of the urban core of coastal cities, while also by moving away from the highly urbanized NSW coastal strip towards more rural, smaller, inland townships. I propose that movement may be underpinned by a mechanism of spatial sorting by individual variation in habitat preferences, which allows mynas to spread across a spatially heterogeneous environments. This is likely be facilitated by diet preferences for natural foods, high neophobia and aggression from a despotic native bird, the noisy miner. Overall, key differences were found between source and front populations along the invasion gradient in behavioural and morphological traits, suggesting that introduced species can provide an excellent case study for examining dynamic invasion processes in real time.

Introduction

In recent centuries, human activity has led to the introduction of a wide range of species into new areas where they were not previously found (Kraus et al. 2003; Lockwood et al. 2013; Mack et al. 2003). These species, often termed alien, exotic, non-native, non-indigenous or introduced species, have the potential to establish breeding populations, spread beyond the original point of introduction and become invasive (Blackburn et al. 2011, 2009; Richardson & Pyšek 2008).

It is now well established that human-mediated invasions by alien species pose a major threat to native biodiversity and human health (Lockwood et al. 2002; McKinney & Lockwood 1999; Pimentel 2011; Simberloff 2004). Although this reality is a global concern, the Australian situation is particularly critical. Given the fact that Australia is an isolated continent with long extinct top predators (Johnson 2006), many human-mediated alien introductions that followed European settlements were successful, and are now causing cause a real threat to native species (Woinarski et al. 2015). For this reason, Australia's 2007 National Pest Animal Strategy flags the need for a more proactive research-based approach to pest animal management that draws on an understanding of the mechanisms of invasion (NRMCC 2007). This thesis addresses this important gap with focus on the common myna in Eastern Australia as a case study.

1. The invasion process

The process of biotic invasion consists of several different stages (Blackburn et al. 2011; Chapple et al. 2012; Duncan et al. 2003) (Fig.1). First, animals need to be transported from their native range and introduced into a new area. These two primary

steps are sometimes deliberate, such as in the case of the introduction of the cane toad (*Rhinella marina*) into Australia to control sugar cane pests (Lever 2001). However, these phases could also be accidental, such as the case of several different ants introduced via global trade with wood and nursery plants (Suarez et al. 2005). Once arrived in a new area, individuals have to survive novel environmental conditions and reproduce over time. This stage is the establishment phase. Following this, a subset of individuals from these established populations succeed in replicating this pattern beyond the introduction area in which they spread. A species becomes invasive when it manages to pass through all the four steps of this progression: transport, introduction, establishment and spread and in has impact on its environment or humans (Fig. 1).

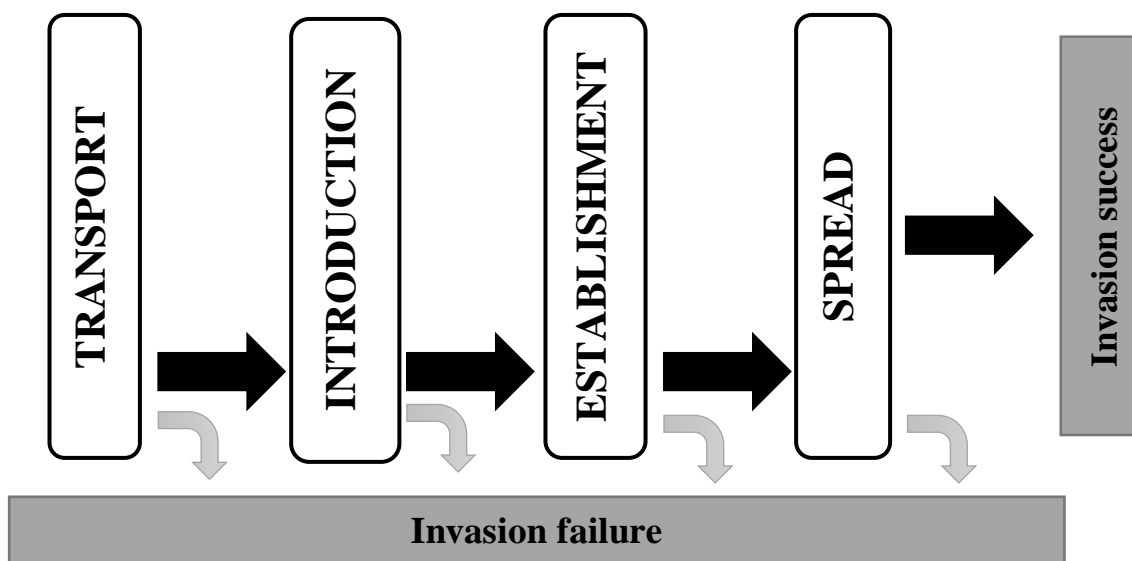


Figure 1. Scheme of invasion process. Inspired from the unified framework proposed by Duncan et al. (2003); Blackburn et al. (2011) and Chapple et al. (2012)

A range of studies have examined the factors that allow introduced species to establish successfully, showing that multiple factors can play a role. These include species-related traits, ecosystem-related characteristics and introduction-related factors (Hayes & Barry 2007; Strayer et al. 2006). Species-related factors include, among other factors, species traits (Blackburn et al. 2009; Shirley & Kark 2009; Sol et al. 2005),

adaptations and pre-adaptations, genetic factors (Ugelvig et al. 2008), size, life history (Sol, Maspons, et al. 2012), behavioural flexibility (Sagata & Lester 2009; Sol et al. 2002) and a diversity of other factors (Cassey et al. 2004; Duncan et al. 2003). Various studies demonstrated the importance of the introduction and the establishment (first stages of the invasion process) to predict, prevent and control novel invasions (Cassey et al. 2004; Duncan et al. 2003; Grevstad 1999; Stearns & Hoekstra 2000).

In Australia, many introduced species have spread and have also become invasive. One of the key challenges for managers and policy makers is to control and restrain ongoing invasions. To face these challenges, a better knowledge of the invasion process is needed. Ongoing invasions offer the very interesting opportunity to study alien populations at different stages of the invasion process. This situation allows scientists to simultaneously explore long-established and recently established populations of alien species in their invading range and to study the mechanisms of range expansion in real time (Chapple et al. 2012; Duckworth & Badyaev 2007; Liebl & Martin 2014).

2. Factors influencing the spread of invasive species

In order to understand the factors facilitating the spread of invasive species in their new range, many studies originally focused on the biotic and abiotic characteristics of the invaded ecosystems (Elton 1958; Evans et al. 2005; Levine et al. 2004; Tilman 2004). These studies showed that novel environments can in some cases provide better conditions for alien species compared to the home range (e.g., more resources, fewer natural enemies and better physical environment) (Liu & Stiling 2006; Shwartz et al. 2009). This concept, named ‘niche opportunities’ (Shea & Chesson 2002), was often underlined as a driver of invasion success (Allington et al. 2013; Le Breton et al. 2005; Macleod et al. 2005; MacLeod et al. 2009).

Both biotic and abiotic factors shape invasion processes and outcomes. One of the main abiotic factors shaping the distribution and the dispersal of a species is climate. Distributional limits of species ranges are generally dictated by temperature and water availability (Coristine & Kerr 2011). Climate directly impacts many species' ranges (Walther et al. 2002). With global warming, the average temperature on Earth is increasing and seasonal patterns are changing, especially in terms of temperature, wind circulation and rainfall, and frequency of extreme events (Hegerl et al. 2018; Mooney et al. 2009; Pachauri et al. 2014). Animals can respond to these climate changes in various ways (Pettorelli 2012). Recent studies have showed that during rapid climatic changes in the past, some species have displayed differential movements instead of moving together (Overpeck et al. 1992; Root et al. 2003). This tearing apart of some communities can lead to population decline and provide new ranges for invasive species (Schneider & Root 2002). Climatic modifications provide opportunities to some invasive species to spread, to extend their home range, or to take advantage of new territories deserted by native species declining or going extinct (Forys & Allen 1999; Herbold & Moyle 1986).

Other important factors that can enhance invasiveness are human-related factors, such as urbanisation and human activities (Gippet et al. 2017; Vonshak & Gordon 2015). Over recent centuries, urbanisation has been continuously increasing, revealing a turning point in 2007 with nearly over half of all humans living in urban areas (United Nations, 2014). This process is expected to accelerate over upcoming decades, introducing even more invasive species in its wake. Human density and urbanisation are driving the spread of many invasive species (Chiron et al. 2009; Moller et al. 2015). When natural habitat is converted to an urban area, this can have positive or negative impacts on different organisms (Goodenough 2010; Simberloff & Holle 1999).

Depending on the species, this change can affect their fitness in various ways, hindering their survival or providing an opportunity. For many species urbanisation equals to the loss of their habitat (Coristine & Kerr 2011; Miller & Hobbs 2002) and those who cannot adapt have to move away or disappear. On the other hand, cities and humans attract some species or provide better resources for them (Kark et al. 2007). Human proximity provides anthropogenic food resources, new ecological habitats (e.g. nest boxes) and changes microclimate conditions (e.g. higher average temperature in city centres than in surroundings) (Jokimäki et al. 2014). Species that benefit from this proximity and thrive in urban areas are sometimes called urban exploiters (Blair 1996; Kark et al. 2007). The number of species favoured by urbanisation is not as numerous as the species highly penalized by the decline of their home range (Marzluff 2001). This imbalance causes a loss of species diversity, consequently human population density is negatively correlated with species richness (Shochat et al. 2006). Few species successfully manage to persist in highly urbanized areas. Invasive species, especially in Europe, constitute a large part of these successful city dwellers (McKinney & Kark 2017). This pattern of dominance by alien species has been observed across several taxa including birds (Chiron et al. 2009; McKinney 2006b), amphibians (Riley et al. 2005), plants (Taylor & Irwin 2004), mammals and reptiles (McKinney 2006a).

2.1. Biologicals traits of alien species

When introduced into a new environment, individuals are confronted with trophic cascades that are often different from those in their native range. Consequently, introduced species must cope with novel food items. New diets may be beneficial or detrimental to their body condition (Huey et al. 2000; Weber & Schmid 1998; Yom-Tov et al. 1999). However, a meta-analysis for invasive species (Parker et al. 2013) demonstrated that while results are not consistent across species, only the World's

Worst invaders (Lowe et al. 2004) were likely to have larger body sizes in introduced ranges compared to their native range.

There is evidence across several groups and regions that body sizes differ across the invasion gradient amongst invaded areas where individuals in front populations show larger sizes than in longer established source populations (Brandner et al. 2018). When introduced into Australia, cane toads first reduced limb length in comparison to their home range (Hudson et al. 2016). Only during the spread phase they begin to gain longer legs.(Hudson et al. 2016). Front individuals with longer legs than toads from long-established (source) populations move further each night (Phillips et al. 2006) and then accelerate the expansion. Cane toad populations on the front of the invasion have longer legs than toads in older (long-established) populations (Phillips et al. 2006). Populations of the African jewelfish (*Hemichromis letourneuxi*) in Everglades National Park (USA) from the invasion front show better body condition (better health) than those of established populations (Lopez et al. 2012). Bigger individuals with longer legs or longer wings are correlated with higher dispersal capacities, and this pattern might lead to a ‘spatial sporting effect’ which has also been termed the ‘Olympic Village effect’ at the invasion fronts (Berthouly-Salazar et al. 2012; Phillips et al. 2010). Therefore, a selection of bigger individuals at the fringe of the invasion range may lead to developing dispersal tendency that can contribute to, and even accelerate, the spread of the species.

2.2. Behavioural traits involved in the invasion process

Behaviour is recognized as an essential component of invasion biology (Holway & Suarez 1999). Various studies have focused on behavioural traits of invasive species (Jeschke & Strayer 2006; Sol et al. 2005) are aimed at understanding how specific behavioural traits enhance invasiveness. The rate at which invasive species spread has

been shown to be related with behavioural traits (Phillips & Suarez 2012). When an invasive species spreads into a new area, individuals need to cope with the novel environment using their own physical capacities and behavioural traits (Shirley & Kark 2009). Introduced individuals also encounter species already present in this environment and are involved in interactions with both native species (Elton 1958; Stohlgren et al. 2003) and other invasive species (Ruscoe et al. 2011; Simberloff 2006; Simberloff & Holle 1999). Therefore, when aiming to understand which behaviours drive the spread of an invasive species and to measure their relative importance in shaping the process, invasive species should be studied at both the interspecific and intraspecific levels.

2.2.1. Interspecific behaviour

Animal populations do not live in a vacuum, they are part of a network of interactions with other species (Duffy et al. 2007; Heleno et al. 2012). Therefore, it is important to take in account their interactions with other species (both native and alien). Species interactions have only been recently recognised as critically important when managing invasive species (Buckley & Han 2014; Lampert et al. 2014). First, they are involved in this network as part of a trophic cascade (Knight et al. 2005). Animal and plant species are part of food webs. One key hypothesis explaining the success of introduced species in the new habitat is the ‘enemy-release’ hypothesis (Liu & Stiling 2006; Shwartz et al. 2009). This suggests that when moving to a novel location, invaders leave their familiar predators behind them and find a new environ without their predators and sometimes parasites, where they can improve their fitness (Keane & Crawley 2002; Maron & Vilà 2001).

In additional to potential lack of predation, introduced individuals may also find new prey and thus diversify their diet. Invasive species often show a broader diet (Weis 2010) in their new range compared with their native range. This position in trophic

cascades (fewer predators and broader diet) is favourable for invasive species and provides them with a good opportunity to establish and spread.

On the other hand, interactions with other species may slow down the establishment of the aliens. Native and other non-native species could be competitors of the invaders (Haythorpe et al. 2013; Holway et al. 2002; Weis 2010). The introduction of an alien species to a new environment modifies the recipient ecosystem (Crooks 2014; Crawl et al. 2008). By being a novel prey, an additional predator or another competitor, the introduced species modifies the existing interaction web (Brown et al. 2011; Frelich et al. 2012). New species interactions arise and, in some cases, local species begin to decrease in abundance as the invader becomes more successful (Clavero et al. 2009). However, over time, native-alien interactions may change. Native species that have survived the arrival of the alien begin to adjust to its presence.

For example, the common planigale (*Planigale maculata*), a small native mammal, has gradually learnt to avoid the toxic alien cane toad (*Bufo marinus*) (Webb et al. 2008). Local species may even begin to benefit from the presence of the alien (Schlaepfer et al. 2011). For example in Hawaii, introduced bird species contribute to dispersing native plant seeds (Foster & Robinson 2007). They help maintain native plant biodiversity and contribute to perpetuating the trophic cascade for native herbivores (Foster & Robinson 2007). Non-native Pacific oysters (*Crassostrea gigas*) colonize un-vegetated tidal flats and form hard reefs, thereby increasing densities of native invertebrate species relative to native oyster beds in several locations on the American coastline (Ruesink et al. 2005). In Japan, non-native plants of the Casuarina family can protect native snails (*Ogasawarana optima* and *O. discrpanis*) against predation by non-native black rats (*Rattus rattus*) (Chiba 2010). In Spain, the alien rose-ringed parakeets (*Psittacula krameri*) are suspected to have negative impact on native

birds. Nevertheless, this species regularly attacks black rats when they climb along the trees to predate eggs and chicks. These attacks result in the death of rats falling on the pavement (9.5% of the aggressions) and some native species may benefit from this antipredator behaviour (Martina 2014). These examples suggest that new ecosystem equilibriums may gradually be reached. At this point removal of the alien could have unexpected, undesirable consequences (Lampert et al. 2014), as in New Zealand where removal of invasive possums (*Trichosurus Vulpecula*) led to a significant increase in invasive rats (Ruscoe et al. 2011). Many studies focus specifically on an invasive species and its negative impact on a native species, in birds (Pell & Tiedemann 1997); in amphibians (Brown et al. 2011); in insects (Rowles & O'Dowd 2006). The science of invasion needs to take into account all the interactions between species involved in an ecosystem rather than considering an alien species in isolation.

2.2.2. *Intraspecific behaviour*

Invasive species have been shown to share several behavioural traits that allow them to establish (Blackburn et al. 2009; Duncan et al. 2003; Holway & Suarez 1999; Kark et al. 2007). For example, many invasive species have been found to display a higher level of activity, exploration and dispersal tendency (see Réale et al. 2007 for review) or to present more aggressive behaviour (Dick et al. 1995; Gamradt et al. 1997) than native species. These outcomes may seem contradictory in the context of the four stages of the invasion process. Some behavioural traits (Table 1), such as the dispersal tendency have a higher contribution to the spread than to the establishment (Cote et al. 2010), while tolerance to humans is more correlated with establishment than with spread (Suarez et al. 2008). This complexity can be explained by inter-individual differences within a population of invaders.

Animals sometimes show inter-individual behavioural differences that are repeatable over time and across situations. (Réale et al. 2007). Within a population, some individuals can display aggressive behaviour while some others do not (Kortet & Hedrick 2007; Réale et al. 2010; Wright et al. 2014). Level of risk-taking differs among individuals, a gradient of shy and bold individuals composes a population (Bell 2005; Kurvers et al. 2010; van Oers 2005). Similarly, social tendencies vary among individuals (Colléter & Brown 2011; Pruitt & Riechert 2009). Such differences between individuals across time and context have become a prominent subject of research. In the literature, stable behavioural traits are referred as personality (Gosling 2001), temperament (Goldsmith et al. 1987) or behavioural syndromes. The term behavioural syndrome is used to refer to a suite of behaviours correlated across situations (Sih et al. 2004). Behavioural traits or behavioural syndromes are now considered to be a possible explanatory factor for the success of invasive species (Blackburn et al. 2009; Chapple et al. 2012).

Some studies have compared behavioural traits and personality in individuals from populations at different stages of the invasion process (Gruber et al. 2017; Gruber et al. 2017; Llewelyn et al. 2010; Lopez et al. 2012; Marsh-Rollo et al. 2012). The mosquitofish (*Gambusia affinis*) shows differences in sociality, demonstrating a personality bias with more asocial individuals on the invasion front (Cote et al. 2010). In western bluebirds (*Sialia mexi-cana*), the individuals on the front of the invasion display a higher level of aggressiveness and a higher dispersal tendency than individuals on the source of the invasion (Duckworth & Badyaev 2007). A possible explanation for these differences between populations is that the individuals that spread might display a different behaviour than the majority of the population. In this case ‘the mean behaviour’ is often less important than the ‘extremes of behaviour’ (Phillips & Suarez 2012).

Table 1. Behavioural traits and their potential effect on the spread of invasive species.
Adapted from Chapple et al. (2012)

Behavioural traits	Spread	Taxa	References
Activity	+	Mosquitofish	(Cote et al. 2010)
Anti-predator behaviour	+	Mosquitofish Crayfish	(Pintor et al. 2008; Rehage et al. 2004)
Tolerance to human	+/-	Birds Ants	(Holway & Suarez 1999; Sol et al. 2002; Suarez et al. 2008)
Dispersal tendency	+	Birds Crustaceans Fishes Cane toad	(Bubb et al. 2006; Duckworth & Badyaev 2007; Llewelyn et al. 2010; Weis 2010)
Exploratory behaviour	+	Fishes Lizards Birds	(Chapple et al. 2011; Cote et al. 2011; Martin 2005; Russell et al. 2010)
Foraging behaviour	+/-	Birds Crustaceans Crayfish Fishes	(Blackburn et al. 2009; Martin 2005; Pintor et al. 2008; Rehage et al. 2005; Weis 2010; Wright et al. 2010)
Habitat preferences	+	Birds Crustaceans Ants	(Blackburn et al. 2009; Lee & Gelembiuk 2008; Suarez et al. 2008; Weis 2010)
Intraspecific aggression	+/-	Ants Crayfish Crustaceans	(Holway & Suarez 1999; Sagata & Lester 2009; Tsutsui & Suarez 2003; Ugelvig et al. 2008; Weis 2010)
Interspecific aggression	+	Ants Geckos Crustaceans Crayfish Crabs Birds	(Duckworth & Kruuk 2014; Holway & Suarez 1999; MacDonald et al. 2007; Rowles & O'Dowd 2006; Usio et al. 2002; Weis 2010)
Nesting behaviour	+	Ants Birds	(Heinze et al. 2006; Holway et al. 2002; Sol et al. 2002; Suarez et al. 2008; Suarez et al. 2005)
Social tendency	+/-	Fish Ants	(Cote et al. 2011, 2010; Tsutsui & Suarez 2003)

3. Avian invasions and the common myna in Australia

Birds provide a good biological model for studying invasive species. Excellent reliable records (number of individuals, introduction dates, etc...) are available from societies and individuals (birdwatchers) around the world, and especially in Australia (Duncan et al. 2003). In this work, I have chosen the common (Indian) myna (*Acridotheres tristis*), a highly invasive passerine across a large part of Australia, as a case study, in order to investigate the invasion process.

The common myna's native range is large, including the Indian subcontinent and parts of Asia (Lever 1987; Sengupta 1982). Non-native populations have been introduced to a wide range of locations around the world (e.g. South Africa, Australia, Hawaii and Israel) (Lever 1987; Fig 2).

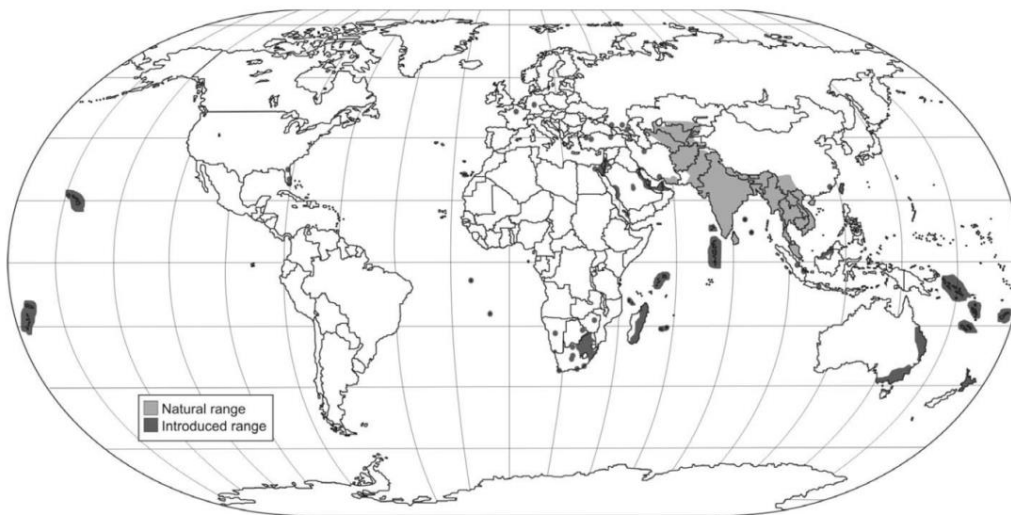


Figure 2. Worldwide distribution of the common myna. Image from Peacock et al. (2007)

The species underwent multiple introductions into Australia, and multiple translocations within Australia, over the course of the XVIII and XIX centuries, each one of which has generated a leading edge of an invasion wave. The first introductions were to Melbourne and Sydney in the XVIII century, after which mynas were translocated to Queensland in the early XIX century and to Australian Capital Territory mid XIX century (Ewart et al. 2018; Gregory-Smith 1985; Hone 1976; Lever 1987). Common mynas are now one of most common birds in urban centers of the East coast of Australia (Parsons et al. 2006; Sol, Bartomeus, et al. 2012) and continue to spread westward (Atlas of Living Australia website <http://www.ala.org.au>) following published climate-matching predictions (Martin 1996). Currently, this species is well established in many cities and towns along the east coast of Australia (Fig 3) (Pizzey & Knight 2007).

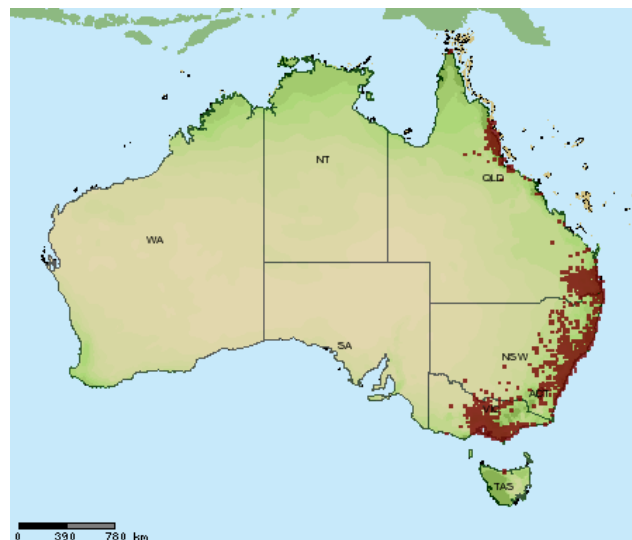


Figure 3. Current distribution of common mynas in Australia. Map from www.birddata.com.au (2005-2007)

The ongoing range expansion of the common myna across the East coast of Australia offers a unique opportunity to explore the mechanisms that drive the spread of an alien species, in real-time. Some populations have been established for decades in the

same place, while others continue to spread and colonize new areas. This situation has enabled us to explore potential behavioural, morphological and ecological differences between populations of birds on the source of the invasion (established over 40 years) and populations of birds in the invasion front (established within the last 10 years).

The common myna shares some biological and behavioural traits with other successful invasive species (e.g. tolerance to human occupied environment, opportunistic nesting behaviour, social tendency). The mynas are urban exploiters in many areas, they are both tolerant to human and vehicles, have a medium body size (average of 110 g) and are generalist for food and habitat (Counsilman 1971). Moreover, common mynas show a larger brain than predicted by their body size (Sol et al. 2002), which is a characteristic correlated with invasiveness capacity (Møller & Erritzøe 2015; Sol et al. 2008, 2005) but see (Healy & Rowe 2007). Common mynas are especially successful in new environment and display innovation capacity (Griffin et al. 2013; Sol et al. 2011). This bird species has seasonal social behaviour. Common mynas form lifelong monogamous breeding pairs and can stay in small family group even after their offspring have fledged (Counsilman 1974). They are usually seen in groups of 2, 6 or 12 but they also join larger groups and spend the night in communal roosts (Counsilman 1973). All this contributes to making common mynas an ideal biological model for the investigation of the factors driving the range expansion of an invasive species.

4. Aims and structure of the thesis

The aim of this research is to study the invasion process with a focus on the final step of the invasion process (the spread), in order to investigate the environmental and behavioural factors that facilitate or impede the expanding range of an invasive species

using the ongoing invasion of common mynas in Australia as a case study. In this body of work, I present five chapters in which I explore biological and behavioural traits of common mynas and compare their distribution and reproduction along the New South Wales (NSW) (and southern Queensland (QLD), Chapter 5) common myna invasion wave. I also consider interactions with native species and their influence on the dynamic of the invasion.

In the two first chapters, I present comparisons of common myna source populations, (defined as those established over 40 years ago) vs. front populations (defined as those established within the last decade). Morphological and physiological differences between source and front populations in common mynas are described in chapter 1. A comparison of behavioural traits (neophobia and sociality) in juvenile front and source common mynas and their potential participation in the mechanisms of the ongoing invasion are discussed in Chapter 2. Chapter 3 is dedicated to a comparative analysis of breeding success and parental care in common mynas and in native parrots, presumed to be the group most affected by the invasive myna (Grarock et al. 2012; Pell & Tidemann 1997) across the NSW common myna invading range. In chapter 4, I examine the potential impact of a highly aggressive native bird, the noisy miner (*Manorina melanocephala*), on the common myna range expansion. In a final chapter (Chapter 5), I investigate the impact of several abiotic factors, including level of urbanisation, and biotic factors, including species richness, on common myna breeding success, and compare this breeding success to that of native parrots. My discussion then summarizes the results of this series of studies and draws a broad picture of factors influencing the spread stage of the invasion process. In the last part of this general discussion, I underline how these findings could improve the control and the management of the common myna in Australia.

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Chapter 1.

Source vs front populations: what shapes the differences?

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Abstract

Invasive species show sometimes differences in morphological traits within their invading ranges or when spreading within their invasive range. These changes could be underpinned by different processes and in many cases, this is not known. Spatial sorting leads to populations presenting enhanced dispersal-relevant traits on the edge of the invasion wave while niche selection and adaptive niche hypotheses lead to populations presenting differences in foraging-related traits within the invading range. The ongoing invasion of common mynas in Australia provides an excellent model to explore which process could be involved in morphological differences within an invading range by offering the opportunity to study simultaneously long-established (source) populations and comparing them with populations on the front of the invasion. In order to explore whether spatial sorting could drive differences in populations of common mynas, we compared some morphological traits related to dispersal (wing measurements, bilateral asymmetry and Hand-Wing Index) in source and front populations of common mynas. We also compared a morphological trait related to foraging ability (beak size) and several health indicators to explore whether differences

in those traits are a cause (niche selection) or a consequence (adaptive niche hypothesis) of the spread of this species. We have estimated the colour intensity of the yellow eye-patches, the concentration of carotenoids in the blood, and the parasite loads (internal and external) of source vs front populations. Birds at the front of the invasions did not exhibit larger body sizes, however they had longer beaks, more colourful eye-patches, higher concentrations of circulating carotenoids and a lower load of external parasites. These findings contribute to tip the balance in favour of foraging related traits and therefore in favour of the niche selection or the adaptative niche hypothesis. However, future research should investigate other front/source replicates in Australia to confirm and precise this pattern.

Key words: invasive species, spread, carotenoids, health, body size, common myna, front and source populations.

Introduction

Invasive species colonize new areas and habitats. One mechanism that has been proposed to support the invasion success of introduced animal species is an increase in body size when invading their new ranges (Roy et al. 2001; Grosholz and Ruiz 2003; Hierro et al. 2005; Hawkes 2007). Parker et al. (2013) demonstrated that while results are mixed across species, only species present on the World's Worst invaders list (Lowe et al. 2004) show larger sizes in introduced ranges relative to the native range. Studies in the marine realm also suggested that an unusual pattern of size change was associated with 19 species of marine and estuarine alien invertebrates (Grosholz and Ruiz 2003) where the majority of species were significantly larger in the introduced range

compared with the native range. In fish, an increasing body size has also been recorded within the invasive range, where individuals participating in the final step (the spread) are larger than their counterparts in the long-established populations. For example, round goby (*Neogobius melanostomus*) in Europe (Brandner et al. 2013; Brandner et al. 2018) and in America (Bergstrom et al. 2008; Gutowsky and Fox 2011) were heavier and larger on the invasion front.

Due to their potential to increase dispersal away from long-settled areas, morphological changes that support higher movement tendencies ('dispersal-relevant traits') have been a particular focus of attention in range expanding alien species. In Australia, following introduction, cane toads showed first a reduction of limb length (Hudson et al. 2016) and then when they range expanded, they exhibited longer limbs on the front of the ongoing invasion with a reduction of sex disparity (Hudson et al. 2016). Front individuals with longer legs than toads from long-established (source) populations move further each night (Phillips et al. 2006) which then accelerates the expansion. Bush crickets (*Conocephalus discolor* and *Metrioptera roeselii*) in the United Kingdom and female (the dispersing sex) common (Indian) mynas (*Acridotheres tristis*) in South Africa are characterised by longer wings on their invasion fronts (Simmons and Thomas 2004; Berthouly-Salazar et al. 2012). It is thought that spatial sorting of individuals along a gradient of individual variation in dispersal-relevant morphological traits hence contributes to creating a moving invasion edge, the expanding speed of which can be accelerated further through the process of spatially-driven associative mating, the 'Olympic village effect' (Berthouly-Salazar et al. 2012; Phillips et al. 2006). There is also increasing evidence that exaggeration in dispersal-relevant traits can incur costs. Longer legs and more movements expose individual organisms to substantial stress; cane toads on the edge of the invasion are more likely to

develop diseases such as spinal arthritis (Brown et al. 2007). For this reason, front toads display enhanced dispersal-relevant traits, but poorer health relative to toads from long-established source populations (Brown et al. 2007).

In contrast to variation in dispersal-relevant traits which forms a selection-neutral process of range expansion, morphological or behavioural traits enhancing fitness have also been considered to be involved in populations' variations within their invading range. Variation in relevant traits (e.g. foraging-related traits) could be present prior dispersal and be a driver of range expansion (niche selection). However, variations could also arise post -colonization induced by natural selection or plasticity (adaptive niche hypothesis), therefore such variations are considered as consequences of range expansion (Berthouly-Salazar et al. 2012). Many alien species are synanthropic (Mckinney 2006) and spread along gradients of urbanization. Different levels of urbanization might select for, or induce (via plasticity), variation in foraging-relevant traits. For example, urban environments with high levels of impervious cover are known to be impoverished in insects (Fattorini 2011). Hence, for alien bird species that spread from areas with more, to areas with less, impervious cover, gradually relying more on probing the soil for insects rather than foraging on human rubbish, one would predict that a trait like beak length should be longer on the front of the invasion wave than in long-established populations. It might also be possible that variation in foraging-related traits is a driver of range expansion in the case where phenotypical variation in foraging-related traits is already present in the source population and each phenotype makes an adaptive decision to disperse from its less favourable habitat towards its most favourable habitat (Travis et al. 2012). Either way, in contrast to exaggeration of dispersal-relevant traits, life in less urbanized environments in birds is associated with better, rather than poorer health (Marzluff 2001; Bradley et al. 2008; Shanahan et al.

2014). This creates a contrasting pattern whereby spread due to exaggeration of dispersal-relevant traits (spatial sorting) is associated with poorer health, whereas spread due to niche adaptation (i.e. phenotypical variation in non-dispersal relevant traits (e.g. foraging-related traits) is a consequence of range expansion or niche selection (i.e. phenotypical variation in non-dispersal relevant traits (e.g. foraging-related traits) is a cause of range expansion) on traits that enhance fitness in less urban environments should be associated with improved health.

Carotenoid-coloured morphological displays provide a window of non-invasive investigation into the diet and health of vertebrate animals (Hill and Montgomerie 1994; Hill 1995; Cook et al. 2013). In birds, coloured signals include red, blue, yellow and orange patches of skin or feathers (Hill et al. 2002; Alonso-Alvarez et al. 2004). Because birds, like other animals, are unable to biosynthesize carotenoids, these pigments must be sourced from the environment either for direct use, or biotransformation into other coloured pigments (Weaver et al. 2018). Carotenoid pigments are used to colour body parts but are also thought to be involved in several physiological functions (McGraw and Ardia 2003) but see (Koch and Hill 2018; Weaver et al. 2018). It is for this reason that the measurement of coloured displays in birds can provide an indication of an individual's dietary intake of carotenoid-rich foods, including insects, and its health (Arriero & Fargallo 2006; Buchanan 2000; Hill 1995) but see (Koch and Hill 2018; Weaver et al. 2018). Measurement of carotenoid displays can be complemented by additional, more traditional measures of avian health, namely parasite loads. For example, the density of feather mites in birds is related to the pool of exploitable resources and serves as an indicator of body condition (Diaz-Real et al. 2014). Similarly the density of oocysts in faeces can be used as baseline intensity of internal gut infection with coccidian (Baeta et al. 2008).

The common (Indian) myna was introduced to Australia mid XIX century to control insect pests around first large human settlements (Melbourne & Sydney) (Hone 1976; Long 1981; Ewart et al. 2018). It is now one of the most abundant avian species in the highly urbanized coastal strip of the New South Wales (NSW) east coast of Australia (atlas of Living Australia, <http://www.ala.org.au>). The species continues to spread westward, however, where its presence is increasingly recorded in small inland townships (www.feralscan.org.au/mynascan). This ongoing range expansion offers the unique opportunity to study comparatively, in real time, long-established (source) and recently-established (front) common myna populations in order to explore the patterns and drivers of the species' spread.

One possible model of range expansion for common mynas in Australia is that spread occurs by spatial segregation of individual birds according to a dispersal-relevant trait, similar to leg length in cane toads. Some support for spatial sorting by dispersal tendency being in operation in common mynas has been gathered from an analysis of wing size within the South African range expansion (Berthouly-Salazar et al. 2012). Female common myna wing size is positively correlated with distance from one introduction site (Johannesburg). Assuming that females are the dispersing sex, as in many avian species, this finding suggests that the South African range expansion is supported by spatial sorting of a dispersal-relevant trait.

One feature of the NSW common myna range expansion, however, is that spread is occurring from the highly urbanized coastal strip to smaller, more rural, townships. Highly urbanised areas provide predictable and abundant anthropogenic food items (Marzluff 2001), but are poor provider of insects and arthropod preys (Fattorini 2011). In line with these general patterns of food availability in urban habitats, east coast urban mynas forage primarily on anthropogenic food sources (Sol et al. 2011). Further, they

select, and fight for, foods high in protein, when given the choice of protein, fat and lipids, providing convergent evidence that they have limited access to protein-rich foods, such as insects (Machosky-Capuska et al. 2015). Given their pattern of spread, mynas in recently established front populations should display body parts that increase their foraging success in less urbanized environments. Several studies have demonstrated that large amount of human refuse in the diet are detrimental to nestling health and development (Pierotti and Annett 2001; Liker et al. 2008). Therefore, mynas in front populations should also be in better body condition than source areas.

The aim of this study was to compare the morphology and health of front and source common mynas within the NSW invasion wave in order to gain insight into the patterns and drivers of spread. According to spatial sorting model, the range expansion of mynas westward from the East coast of Australia could be underpinned by differential movement across the landscape due to individual variation in dispersal-relevant morphological traits. Under this model, we predicted that front mynas would have longer wings, and be in poorer bodily health condition with higher parasite loads than mynas from source areas. According to niche selection model, the common myna invading range expanding westward from the highly urbanized coastal strip of central NSW towards smaller inland townships could be underpinned by variation in foraging morphology relevant to success in less urbanized environments. According to the adaptive niche hypothesis, differences in foraging-relevant traits could also be a consequence of settlement in new areas (selection or plasticity). Under both of these models, we predicted that front mynas would show longer beaks and be in better health with lower parasite loads than source mynas (Fig 1).

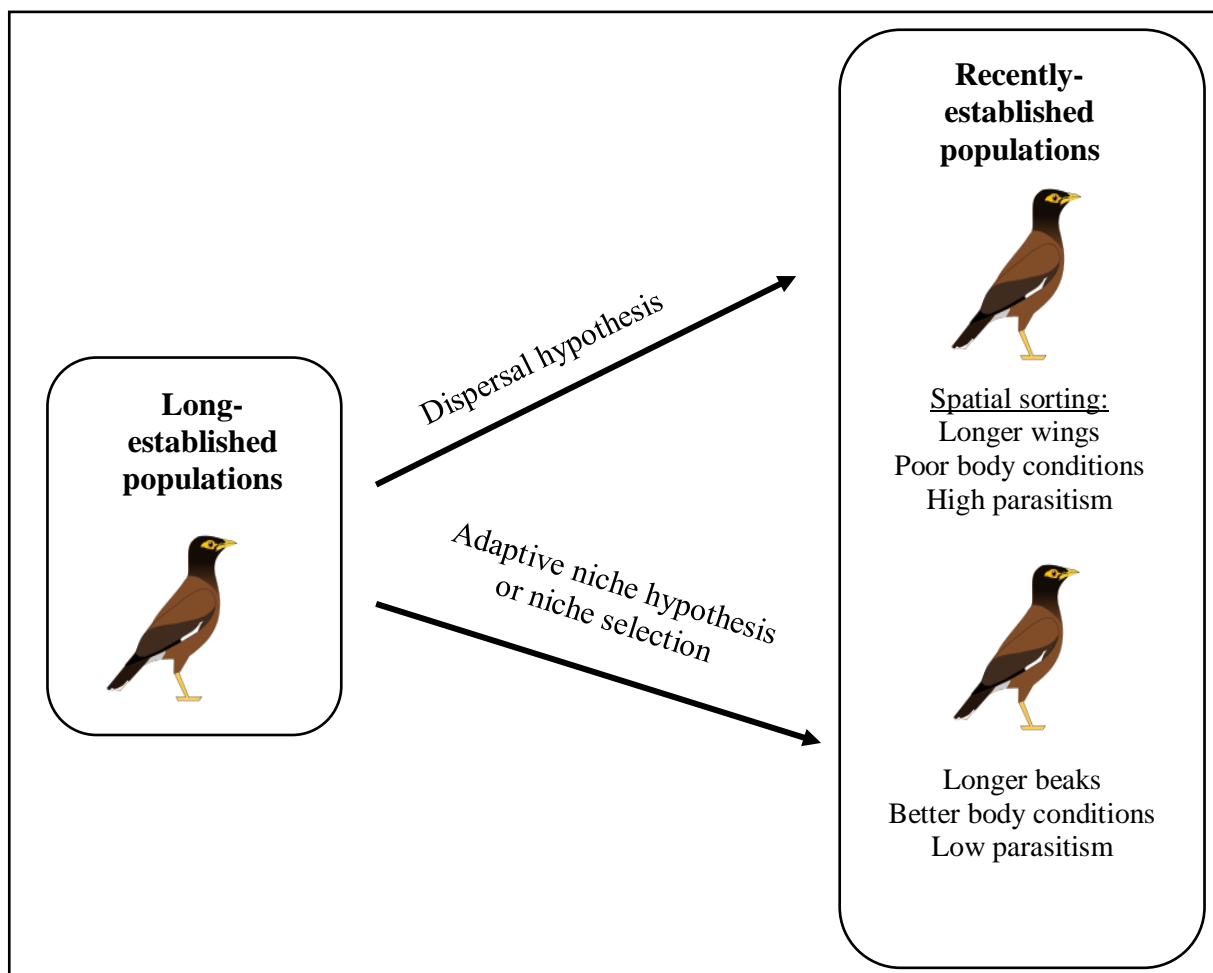


Figure 1. Hypotheses predicting common myna phenotypes in recently established-populations.

Methods

Study area, trapping and housing

During autumn 2017 (01/05/2017 to 13/06/2017), fifty common mynas (Table 1) were captured in different locations in New South Wales, Australia, using a walk-in baited trap specifically designed to trap this species (Tidemann 2005; Griffin 2008). Twenty-five mynas from old established source populations were trapped in four sites within the larger agglomeration of Sydney (Fig 2), where mynas have been breeding since the beginning of the last century (Hone 1976). Fourteen invasion front mynas were captured

in two different sites in Tamworth and eleven other invasion front mynas were trapped in Krambach (Fig 2), where mynas have only been breeding for the last ten years (Atlas of Living Australia, <http://www.ala.org.au>, see more details in McKinney and Kark 2017). Birds were transported by car in small individual cotton bags to the Central Animal House at the University of Newcastle where they were held for an entire night in individual indoor cages (0.5 m x 0.5 m x 0.6 m) with ad libitum food (dog pellets) and water. The following morning, some droppings from each bird were collected and kept for analyses. After morphological and physiological measurements, groups of five to eight birds were housed in outdoor aviaries (1.95 m x 2.2 m x 1.0 m).

Table 1: number of birds trapped breakdown by the stage of the invasion, the sex and the age.

	Long-established populations	Recently-established populations
Number of juvenile females	8	6
Number of adult females	6	4
Number of juvenile males	3	3
Number of adult males	8	12

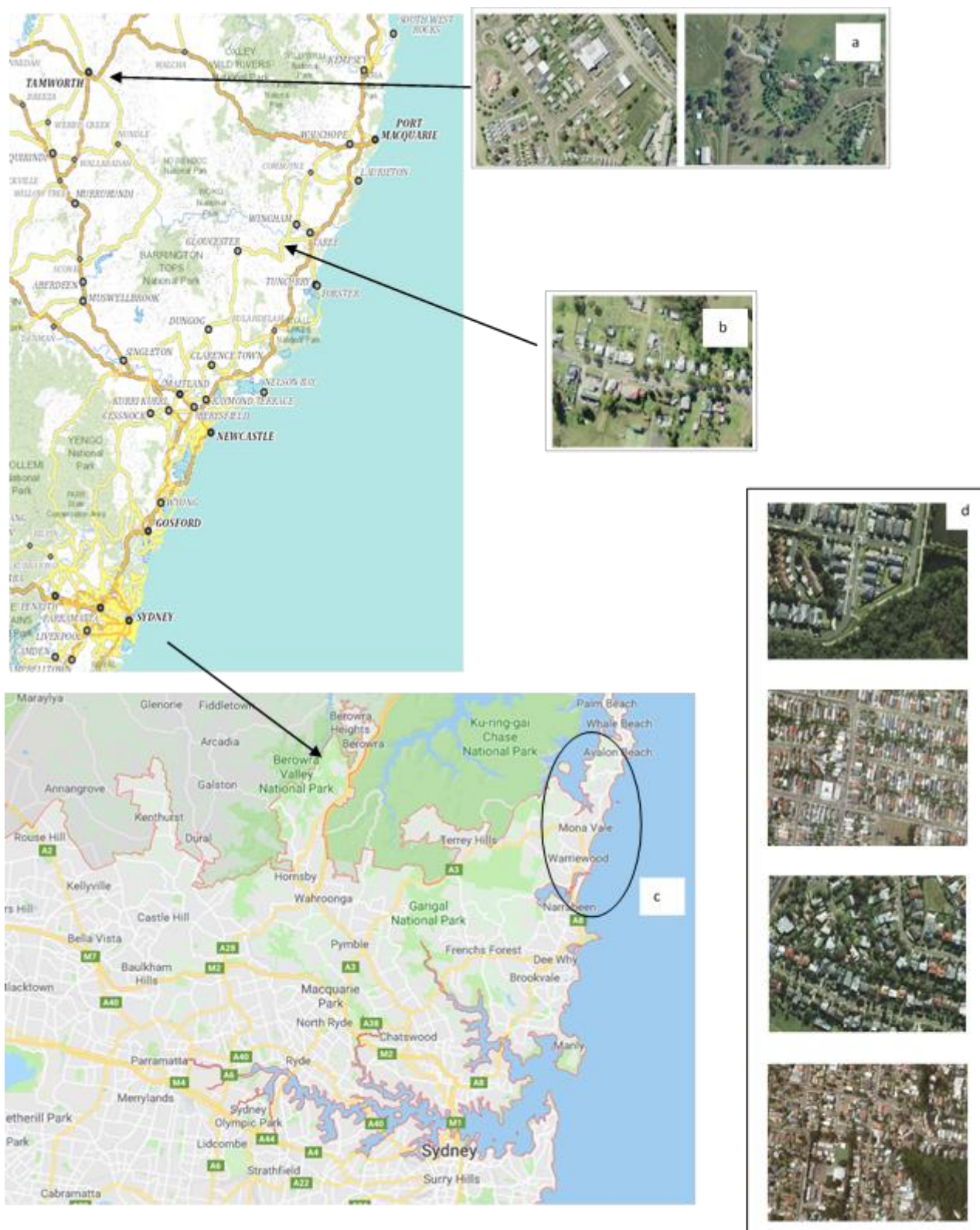


Figure 2. Trapping locations. (a) Trapping sites in Tamworth (front of the invasion). (b) Trapping site in Krambach (front of the invasion). (c) Trapping area in the Sydney (source of the invasion). (d) Trapping sites in Sydney.

Morphological measurements

The day after their capture, birds were weighed and measured (beak, tarsus and wing, Appendix 5). For consistency, a single investigator (FL) took all the morphological measurements. In order to estimate the asymmetry of each individual, measurements of both tarsus and both wings were recorded and the absolute difference in left-right lengths was calculated. As a higher flight capacity is correlated to dispersal ability in birds (Claramunt et al. 2012; Weeks and Claramunt 2014; Hosner et al. 2017), we also calculated the Hand-Wing Index (HWI), (Appendix 5) using the standard length of the closed wing (WL) and the distance from the carpal joint to the tip of the first secondary feather (SL) (Claramunt et al. 2012).

$$HWI = 100 \times \frac{WL - SL}{WL}$$

While male mynas are slightly heavier than females, mynas are not sexually dimorphic in plumage, so two feathers were collected from each bird in order to send it to a commercially available company to obtain a DNA-determined sex (<https://dnasolutions.com.au/>). Juveniles were identified based on their brown plumage and black markings on their cover feathers (Counsilman 1971).

Coloured signals and carotenoids

Inter-individual differences in the color of the eye-patch were determined by analyzing photos of the birds' head at the time of capture. The photos were taken in a standardized environment (Fig 3). The device consisted of a box (13 × 36 × 13 cm; W × H × D), painted black on the outside (to avoid light penetration through the walls), with a digital camera attached on the top, a source of light fixed on the inner side of the lid and a

horizontal transparent plastic panel set-up inside the box at 19 cm from the lens of the camera. The bird was introduced in the bottom part of the box and the left side of its head was held against the plastic roof. The left side eye-patch and part of the bill were placed under a small opening ($2.5 \times 0.2 \times 1.5$ cm), so there was only air between the lens of the camera and the eye-patch/bill. Color and gray standards were placed on the opposite side of the glass panel, as well as a ruler (size standard). Two photos of the left side of the head were taken for each bird and analyzed with a custom-made MATLAB program. RGB values of the eye-patch were recorded and a mean value between the two pictures of each bird was taken.

The color of the eye-patches allowed us to measure the level of carotenoids allocated to by individuals to coloured displays. Additionally, we collected blood samples from each bird to estimate the level of circulating carotenoids before metabolization and allocation to various biological processes. The blood was immediately centrifuged (5 000 g, 15 min) to allow collection of the plasma. The plasma was then stored in 1.5ml Eppendorf tubes at -80°C for later analysis. The carotenoid concentration was analyzed using a standardized colorimetric technique (see Alonso-Alvarez et al. 2004). 20 μl of plasma was diluted in 180 ml of absolute ethanol, mixed with a vortex and centrifuged (1 500 g, 10 min) to precipitate the flocculent proteins. The supernatant was analyzed using a spectrophotometer to determine the optical density of the carotenoid peak at 450 nm. Carotenoid concentration were determined from a standard curve of lutein.



Figure 3. Photos of the left side of the head of two common mynas with different eye-patch coloration in the homemade photo-box with the color and gray standards.

Parasites (external & internal)

The level of external parasitism was assessed by estimating the number of mites attached to the primary and secondary feathers of the extended right wing exposed to a lamp. A score was established as a function of mites' abundance on primary and secondary feathers of the wing. The abundance was scored as A (no mites), B (low presence of mites on primary or secondary only), C (low presence on both primary and secondary or high presence only on one type of feathers), D (low presence on one type and high presence on the other) and E (high presence on both primary and secondary feathers).

Counts of coccidia oocyst in the faeces were used to estimate individual internal parasite load. All samples were collected between 8.00 and 10.00 am during the first morning after arrival at the holding premises. Two grams of fresh faecal samples were collected with the insert of a Fecalyzer® before being placed in the fecalyzer container. A small quantity of faecal suspension solution (sodium nitrate) was added to help

dissolve and break-up the sample. Once the sample was thoroughly mixed into the fecalyzer, the container was filled up to the top with an eye dropper to create a meniscus (bulge of water that extends up over the edge of the container). The sample was then left to sit for 10 to 15 minutes to allow parasite eggs, which are lighter than the saline solution to float to the top. A slide cover glass was put on the top of the meniscus to allow the fixation of oocysts onto the glass. The cover glass was then transferred to a slide and the sample was analyzed under a 10X lens to record the presence of coccidia oocysts and a category was used to quantify their abundance. Category A = absence of parasites; $0 < \text{category B} < 5$ oocysts; $5 < \text{category C} < 10$ oocysts; category D > 10 oocysts. All procedures and protocols were approved by the University of Newcastle Animal Care and Ethics Committee (Animal Research Authority n° A-2014-424).

2.3 Data analysis

In order to compare morphologic measurements in populations of common mynas we created an overall body size index using a principal components analysis (PCA). The first axis explained 61.7% of the variance and thus could be considered a good summary of the data. The score generated by the analysis reflected all the data used in the analysis: wing (0.53), tarsus (0.52), weight (0.51), and beak (0.42). Variable loadings indicated that individuals with higher scores were overall larger birds. As these scores were normally distributed and were analysed using a linear regression model using the R package lme4 (Bates et al. 2014). The full model contained the invasion stage (source/front populations), the sex of individuals, their age (adult/juvenile) and the interactions between invasion stage and sex, and between invasion stage and age. Non-significant interactions were removed successively; we decided to keep the factors

invasion stage, sex and age regardless of their significance in the final model. This methodology was applied to all models presented in this study. To compare body part differences, we used the same model to explore potential differences in the size of the beak, the size of the right wing, and the hand-wing index (HWI) between populations. To explore potential differences in symmetry (wings and tarsus), we compared the absolute difference $|\text{left-right}|$ with the non-parametric independent samples Mann-Whitney U test.

Eye-patch pictures generated three variables (Hue, Chroma and Brightness). We compiled these variables in a PCA to generate a score reflecting the inter-individual differences in eye patch coloration. The first axis explained 67.2% of the variance and thus was considered as a good summary of the data. The score generated by the analysis reflected all the data used in the analysis: Hue (0.69), Chroma (-0.62) and Brightness (0.35) (Fig 5). Hue reflects the level of different wavelengths; in this case high scores represented yellow spectrum and low scores represent red spectrum; Chroma reflects the intensity/concentration of the colour. Higher scores on first axis reflected less colourful eye-patches with less red component (less carotenoids). We used the scores provided by the first axis to fit a full linear regression model. Invasion stage (front/source), sex, age and their interactions were entered in the model.

The same model was used to explore potential predictive factors for the level of carotenoid in the blood. Internal and external parasitism were evaluated with a score, so we used a chi squared test to compare the parasite load between populations. All statistical tests were carried out using SPSS 24 (SPSS Inc., Chicago, IL, U.S.A.) for the non-parametric tests, R v3.4.3 (2017) for the linear models and JMP 13 for the PCAs. Two-tailed tests were used throughout and alpha levels were set at 0.05.

Results

Morphological measurements

Age and sex, but not invasion stage (front vs. source), were significant predictors of myna body size (body index) and wing size (Table 2). Males had larger body indices and longer wings than female mynas. Although adults tended to have longer beaks than juveniles and males longer beaks than females, invasion stage (front vs. source) was a stronger predictor of beak size than age in a model containing both predictors (Table 2). Common mynas from the front of the invasion had longer beaks than common mynas from long-established populations (Table 2, Fig 4).

Table 2. Linear regression models with all dependent variables used for body measurements in front and source common mynas.
(Nsource=Nfront=25; Nmale=26,Nfemale=24;Nadult=30,Njuvenile=20)

Variable	Factor	F	P
Body index	Invasion stage	1.308	0.259
	Sex	68.962	<0.001
	Age	20.934	<0.001
Wing	Invasion stage	0.545	0.464
	Sex	12.948	0.001
	Age	9.960	0.003
Beak	Invasion stage	10.460	0.002
	Sex	6.235	0.016
	Age	3.937	0.054
HWI	Invasion stage	1.317	0.257
	Sex	0.263	0.610
	Age	1.020	0.318

The table presents simplified models (interactions were removed because non-significant). Bolded p-values were below a 0.05 threshold of significance

Independent Samples Mann-Whitney tests revealed no differences in morphological asymmetry of any body part between front and source mynas (wings: $U=333$, $N(\text{front}) = N(\text{source})=25$, $p = 0.649$; tarsus: $U=313$, $N(\text{front})= N(\text{source})=25$, $p = 0.992$).

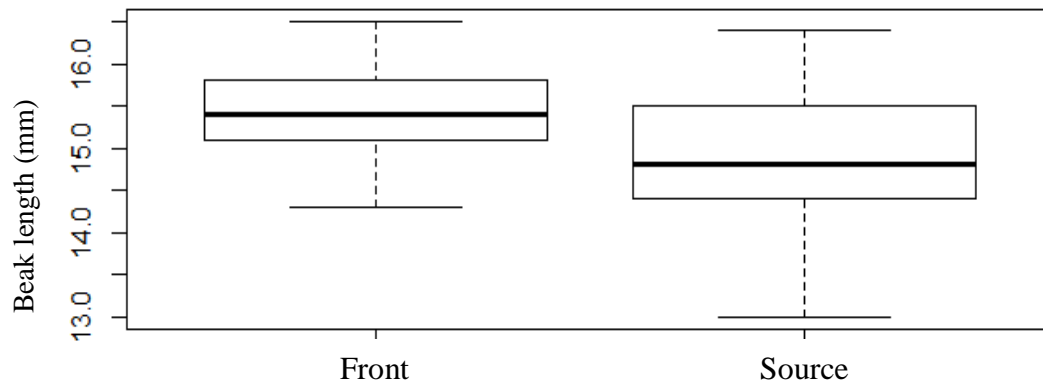


Figure 4. Boxplots of beak length measured in front and source populations of common myna ($N(\text{source}) = N(\text{front}) = 25$). The line within each box represents the median length, the upper and lower borders of each box are the 25th and 75th percentiles and the lower and upper bars are the 10th and 90th percentiles.

Coloured displays and carotenoids

Front and source, and adult and juvenile, common mynas showed significant differences in their colourful displays and in circulating concentrations of carotenoids. Invasion stage and age were significant predictors of the eye-patch colour-index (Table 3, Fig 5a). Front mynas showed lower values on the first PCA axis (Table 3, Fig 6) indicating a higher level of colour intensity with more red component in their eye-patches than birds from source populations. Similarly, front and adult mynas presented with significantly higher levels of circulating carotenoids than source birds and juveniles (Table 3, Fig 5b).

Table 3. Linear regression models on eye patch color display (color index, PC1) and concentrations of circulating carotenoids. (N_{source} = N_{front} =25; N_{male}=26, N_{female}=24; N_{adult}=30, N_{juvenile}=20).

Dependent variable	Factor	F	P
Colour index	Invasion stage	34.035	<0.001
	Sex	1.114	0.299
	Age	4.986	0.032
Carotenoids	Invasion stage	7.084	0.012
	Sex	.819	0.372
	Age	4.584	0.040

The table presents simplified models (interactions were removed because non-significant). Bolded p-values were below a 0.05 threshold of significance.

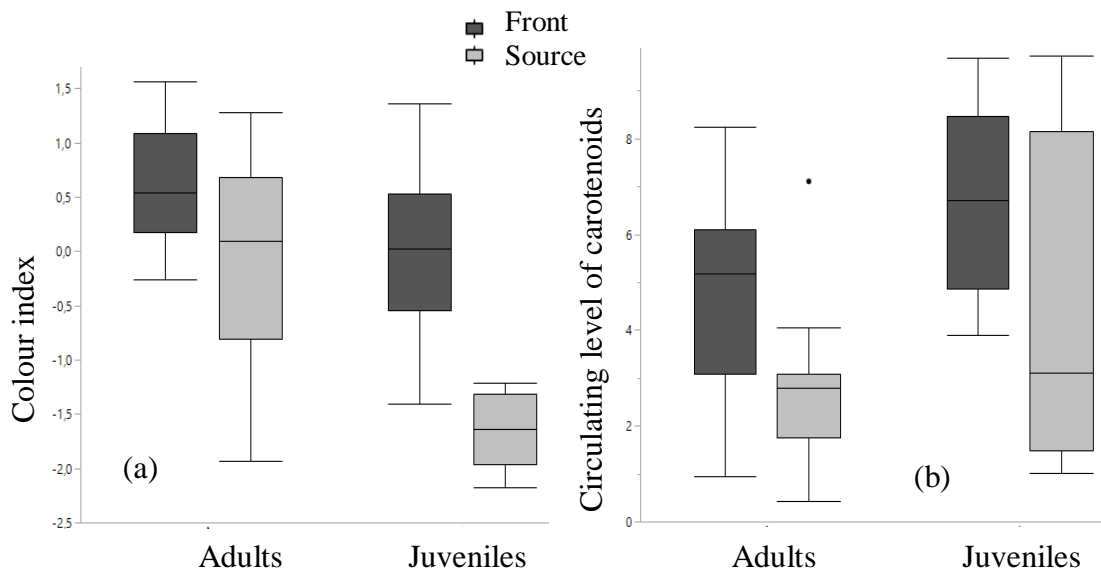


Figure 5. (a) Boxplots of colour index (PC1) measured with eye-patch photographs in front and source common myna. (b) Boxplots of circulating levels of carotenoids in front and source common mynas. N_(source) = N_(front) =25. The line within each box represents the median values, the upper and lower borders of each box are the 25th and 75th percentiles and the lower and upper bars are the 10th and 90th percentiles

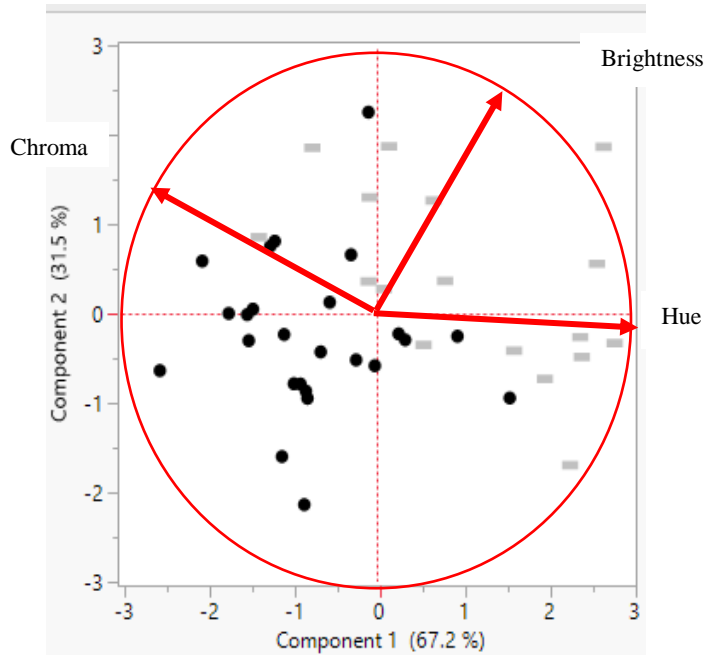


Figure 6. Graphic representation of the PCA on the three measurements extracted from the eye-patch pictures (Hue, Chroma and Brightness). Black dots represent front birds and grey rectangles represent source birds.

External & internal parasites

Birds from the two populations showed no difference in levels of internal parasitism (chi-square = 6.88, df = 4, $p = 0.142$), but displayed a significant difference in their level of external parasitism. Birds from the source population had more mites on their wing feathers than birds from the front of the population (chi-square = 10.6, df = 4, $p = 0.031$) (Fig. 7).

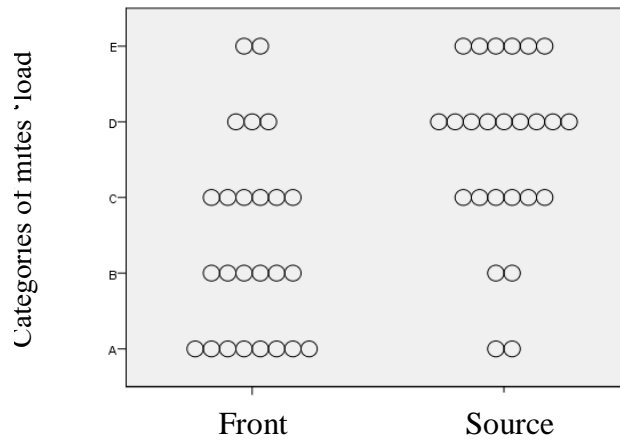


Figure 7. Number of individuals per category of external parasites load in front and source populations. Category A represent individuals without mites and category E individuals with the highest level of external parasitism.

Discussion

Comparing long and recently-established populations of common mynas in NSW Australia, we demonstrated that invasive common mynas display morphological and health differences across their invasive range. Common mynas in areas on the edge of the inland NSW invasion front, where the species has been breeding for less than a decade, showed longer beaks than those from areas on the NSW east coast, where mynas have been breeding for more than 40 years. In addition, these ‘front’ mynas displayed more colourful eye patches, presented with higher concentrations of circulating carotenoids, and carried fewer external parasites. In contrast, front mynas did not exhibit enhancements to dispersal-relevant traits, such as wing length or the Hand-Wing Index and, if anything, appeared in better health than source mynas. These findings point towards an involvement of traits relevant to enhancing fitness in less urbanized landscapes (front of the NSW invasive wave) and seem to support the niche

selection or the adaptive niche hypotheses rather than the dispersal hypothesis that should enhance dispersal traits on the front of the invasion.

The common myna invasion of eastern NSW is currently progressing from the highly urbanised coastal strip westward towards smaller, more rural, townships. The present finding that ‘front’ mynas have longer beaks strongly suggests that birds forage more heavily on natural food items in townships where the species has begun colonizing only recently. These small cities (e.g. Tamworth) and towns (e.g. Gloucester) typically have smaller urban cores, larger suburban gardens, and subside more quickly to surrounding rural landscapes than the more intensely urbanized NSW coastal strip. It is quite possible that these smaller cities on the invasion front provide a greater abundance of natural prey, such as insects, which are known to be an important element of common myna diet, particularly for nestlings, in its native range (Sengupta 1976). In contrast, city mynas are known to forage primarily on anthropogenic rubbish (Faeth et al. 2005; Crisp and Lill 2006; Shochat et al. 2010; Sol et al. 2011). Further, they select preferentially, and show high aggression around, high-protein food sources, suggesting limited access to protein-rich foods, including insects (Machovsky-Capuska et al. 2015).

The hypothesis that mynas on the NSW invasion front rely less on anthropogenic foods than source birds was supported by the finding that front individuals have more colourful eye-patches and higher levels of circulating carotenoids. Carotenoids are biologically active pigments that cannot be synthesized *de novo* by birds. Consequently, these pigments have to be obtained directly from the diet or produced by biotransformation of dietary xanthophylls (Hill 1996; Hill 2000). Several studies in captivity have demonstrated that supplementation of carotenoids enhances colouration of feathers (Hill 2000; McGraw et al. 2001; Peters et al. 2008) and bill (Jouventin et al. 2007; Baeta et al. 2008; Giraudeau et al. 2011). On the other hand,

nutritional deficiencies of carotenoids tends to lead to less pigmented feathers, beaks and eye lore skin (Hill and Montgomerie 1994; Shawkey et al. 2006; Pérez-Rodríguez and Viñuela 2008). Urbanized areas and those with high levels of pollution are often described as poor-quality habitats in comparison to more natural and rural habitats (see Shanahan et al. 2014 for review). Rural areas are overall richer in insects and therefore form environments richer in carotenoids (New 2018). A link between urban life and reduced carotenoid intake is supported by habitat-comparisons indicating that birds from rural habitats are more colourful than birds in urbanised areas (Hörak et al. 2001; Isaksson et al. 2005; Biard et al. 2006; Jones et al. 2010; Giraudeau and McGraw 2014), but see (Koch and Hill 2018; Weaver et al. 2018). Hence, changes in colouration and circulating carotenoids in mynas at different stages of invasion are consistent with a pattern of spread from highly urban to less urban landscapes.

In many bird species, carotenoid display colouration provides an honest signal of body condition and health (Iverson & Karubian 2017; Lifshitz & St Clair 2016; Weaver et al. 2018 but see Koch & Hill 2018). Thus, ‘front’ mynas were not only more colourful, they also appear to be healthier. This idea is supported by the finding that they exhibited significantly fewer external parasites (mites) than mynas from long-established source areas. Mites spread easily from one host to another by contact without any intermediary; this type of contamination is highly favoured by the roosting behaviour of common mynas when a lot of individuals congregate to spend the night in the same tree (Counsilman 1971; Counsilman 1973). Urban areas are now well-known for harbouring higher bird densities than less urbanised ones (Moller et al. 2012), and these higher concentrations of birds are likely to present more propitious conditions for mite proliferation. Mite loads have also been shown to be a better predictor of coloration and of relative body condition than pectoral muscle condition (Harper 1999).

Our study corroborated this observation by showing that common mynas in recently-established populations, which have more colourful eye-patches, also present with lower mite loads. More research is needed to investigate the unexpected finding that ‘front’ mynas did not present with lower levels of internal parasites, a feature often associated with brighter bare skin displays (Iverson and Karubian 2017). Recent reviews on carotenoids in avian species (Koch and Hill 2018; Weaver et al. 2018) have revealed that relationships between available carotenoids in the diet, colouration, immune system and therefore body condition are complex. The conversion of dietary carotenoids into metabolized carotenoids seems to be the most important factor, regardless to the amount of dietary carotenoid intake (Weaver et al. 2018). Then, metabolized carotenoids are allocated to coloured signals or to the immune system. However, this hypothesis is true when individuals have access to enough carotenoids in their habitat. Source common mynas presenting less colorful eye-patches and more mites may undergo a lack of dietary carotenoids or may prioritize dietary carotenoid allocation to their immune system because of their higher external parasite load.

In South Africa, common myna spread away from one point of introduction, namely Johannesburg, has been linked to spatial sorting of females, the dispersing sex, along a gradient of wing length and head size, a proxy for brain and cognition (Berthouly et al. 2012). However, variation in foraging morphology did not correlate with distance from the introduction point (Berthouly et al. 2012). Hence, in South Africa, myna spread is assumed to result from spatial sorting of the dispersing sex according to variation in traits that increase dispersal into, and fitness within, novel environments, whereas changes in foraging morphology result from local adaptation to recipient environments (Berthouly et al. 2012). Foraging traits like beak size and beak shape are strongly linked to diet and foraging niche (Willson et al. 1975; Grant and

Grant 2002). Beak length is strongly associated with feeding practices. For example, short bills occur in species using gleaning feeding techniques, while longer beaks occur in species that pursue hidden and difficult-to-access prey (Leisler and Winkler 2015). These changes in beak morphology can arise in less than a decade of breeding. Genetic studies on Darwin finches (genus *Geospiza*) demonstrated the high heritability of the size and the shape of the beak (Boag 1983; Keller et al. 2001; Abzhanov et al. 2004; Grant and Grant 2006) and the rapidity with which natural selection on beak morphology can occur (Amichhaney et al. 2018). Hence, we can assume that similar speeds of adaptation can occur in mynas and that longer beak lengths arise post-colonization. However, we cannot exclude that the change in beak size had already occurred before the spread of individuals on the front of the invasion.

There is also growing evidence that beak size plays a significant role in body temperature regulation in many avian species (Tattersall et al. 2009; Symonds and Tattersall 2010; Ven et al. 2016; Tattersall et al. 2017). Therefore, differences in temperatures in similar habitats could lead to different beak sizes within a species. Recent studies have illuminated the role of climate with the role winter temperatures and especially humidity in the evolution of bird beak size in passerines (Gardner et al. 2016) and in honeyeaters (Friedman et al. 2017). Colder winters and hot and humid summers seem correlated with smaller beaks (Gardner et al. 2016; Friedman et al. 2017). In our study, all birds were trapped in locations undergoing a humid subtropical climate, even if there our study front sites (Tamworth and Krambach) exhibit colder temperatures in winter than source sites in Sydney (Climate-Data.org). A study focused on 36 species of Australian passerine demonstrated that gradient of humidity was the most important factor involved in beak size (Gardner et al. 2016). Since front and source populations of common mynas experience a similar level of humidity, the

difference in temperatures are not important enough to modify the size of the beak. Differences in food quality and availability are probably a more important driver. However, modifications may have not appeared already. More research, at a larger scale, is needed to explore the effect of climate on common myna beak size.

One question remains: is variation in foraging preferences is a cause or a consequence of spread? In other words, do mynas spread across heterogenous habitats accordingly to their foraging preferences (variation for anthropogenic or more natural food sources); or, is dispersal away from source sites random and selective forces within recipient environments shape foraging preferences post-establishment.

Conclusions

Common mynas differ in morphology and health along their invasive range from source to front populations. Differences in parasite load, in their levels of circulating carotenoids and in the coloration of the eye-patches are most likely induced by higher intakes of insects, potentially facilitated by longer beaks suited to propping for insects in the ground. Taken together the results presented here are not consistent with a model by which the current inland spread of mynas across Eastern Australia is the result of spatial sorting, they are more consistent with models of range expansion build on niche selection or niche adaptation. Common mynas may be spreading from long-established habitats to seek more suitable food items and then colonizing new habitats on the front of the invasion via a mechanism of phenotypical matching (niche selection). Alternatively, individuals may spread randomly regarding to foraging-related traits and therefore variations on those traits are a consequence of the establishment on the front of the invasion. Future research should attempt to tease apart the two latter

hypotheses, while also studying other front/source replicates in Australia to confirm observed patterns.

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Chapter 2

Who are the colonizers? Common mynas differ in neophobia across the two extremes of the invasion wave

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Abstract

Behavioural traits predicting and supporting the success of invasive species have been an important focus of research effort in the field of invasive science over the recent two decades. However, the mechanisms by which these traits contribute to the invasion process are poorly considered. One emerging hypothesis is that each stage of the invasion process (transport, introduction, establishment and spread) might require different behavioural traits or different levels of the same traits. To test this hypothesis, a growing, but still small, amount of work is comparing populations at different invasion stages (e.g. establishment versus spread), but clear patterns of population differences in support of the hypothesis have yet to emerge. So far, sociality and risk-taking are amongst the traits that yield the most consistent patterns across taxa. The ongoing invasion of common mynas (*Acridotheres tristis*) in Australia provides the opportunity to investigate simultaneously individuals from an invasion source (established > 40 years) and an invasion front (established < 10 years) and to explore whether they differ in behaviour. We conducted a captive study on juvenile wild caught common mynas and compared their level of neophobia and sociality across their invasive range. We discovered that young individuals were more fearful of novel

objects in front populations than in source populations but did not show differences in tolerance of humans and in their level of sociality. Our results support the hypothesis that variation in one behavioural trait, namely neophobia, may play a role in driving the myna's invasion of Australia's east coast invasion, with more neophobic individuals moving to invasion front.

Key words: invasive species, invasion process, neophobia, sociality, common myna.

Introduction

Biological invasions have been suggested to be a source of biotic homogenization (McKinney and Lockwood 1999; Shochat et al. 2010) and one of the greatest threats to biodiversity along with habitat destruction (Wilcove et al. 1998; Bellard et al. 2016). Substantial research investment has been successful in identifying various ecological (e.g. biotic resistance; enemy release; novel weapons) and demographic (e.g. propagule pressure) processes, as well as life-history traits (e.g. broad diets; rapid dispersal; high reproductive rates), associated with invasion success (Cassey et al. 2004; Chiron et al. 2009; Dyer et al. 2017; McKinney and Kark 2017). However, far less is known about the behavioural traits that predict invasiveness of animal species (Duckworth & Badyaev 2007; González-Bernal et al. 2014; Pintor et al. 2009; Truhlar & Aldridge 2015a). Further, in most cases where behavioural predictors have been a research target, how these traits contribute to increasing invasiveness remains mostly speculative (Duckworth 2006; Duckworth & Badyaev 2007).

Exceptions are two keystone studies which have revealed the mechanisms by which behaviour can enhance invasiveness. First, the highly invasive Argentine ant (*Linepithema humile*) exhibits significant territorial defense with a high level of intraspecific aggression in its native range. When invading new territories, individuals

display a loss of intraspecific aggression, followed by a breakdown of territoriality (Holway et al. 1998), allowing individuals to aggregate in super-colonies, which become numerous and more competitive than native ants, and in turn, very successful invaders (Holway and Suarez 1999). Second, male Western bluebirds (*Sialia mexicana*) reared amongst high densities of conspecifics show heightened levels of aggressiveness relative to males reared in low density areas (Duckworth & Badyaev 2007). Upon dispersal into areas previously unoccupied by Western bluebirds, the heightened aggressiveness of these pioneers allows them to displace already established mountain bluebirds (*Sialia currucoides*) from desirable breeding territories in invade the new area. As Western bluebirds' population sizes grow and begin to replace mountain bluebirds, mean male aggressiveness decreases once again within a few generations. These examples illustrate how behaviour can intricately influence and support invasiveness.

In animals, the invasion process consists of four stages: transport, introduction, establishment and spread (Blackburn et al. 2011; Chapple et al. 2012). A discussion initiated in the late 1990s (Holway and Suarez 1999), raised the idea that behavioural traits influencing success at one stage of the invasion process might differ from those shaping the success of individuals at another stage of the invasion. For example, the ability to forage in the dark might help certain fish to survive in ballast tanks during transport, but could impede their establishment if they are released in clear water (Kolar and Lodge 2001). In alien birds, tolerance to humans is a trait more correlated with establishment than with the spread (Suarez et al. 2008). Other traits currently predicted to contribute to spread more than to establishment include a high dispersal tendency, high activity and high boldness, along with low sociability (e.g., Chapple et al. 2012; Chapple and Wong 2016).

Thanks to research comparing populations at different invasion stages, evidence in favour of the involvement of behaviour in invasiveness is slowly emerging. Mosquitofish (*Gambusia affinis*) from front populations are less social than their counterparts from long-established populations. Cane toads (*Rhinella marina*) on the edge of the invasion front display an enhanced dispersal ability and locomotor performance mediated by longer legs and greater physiological endurance relative to cane toads from old-established populations (Phillips et al. 2006; Llewelyn et al. 2010). In sparrows (*Passer domesticus*), bolder birds were found in front populations and shyer ones in long-established ones (Martin 2005). But patterns are not always so consistent. For example, invasive waxbills (*Estrilda astrild*) show no evidence of an involvement of boldness: differences in behaviour (exploration, sociality) correlate with the climate seasonality and not invasion stage (Carvalho et al. 2013). Similarly, killer shrimps (*Dikerogammarus villosus*) show no difference in boldness or sociality between populations from the centre and the fringe of the invasion (Truhlar and Aldridge 2015b). Thus, the current body of comparative research is still too small to draw general conclusions about the relevance of specific behaviours to the invasion process more generally. What is needed now is to expand the range of invasive animal species in which behavioural studies are undertaken so that, in the long term, we can determine whether general behaviour-invasion relationships that hold within or perhaps even across taxonomic groups emerge (Chapple et al. 2012). This was the research gap the present research aimed to contribute to fill.

The ongoing range expansion of the common myna (*Acridotheres tristis*) along the Eastern coast of Australia, as well as westward from the Eastern seaboard, provides an excellent opportunity to explore the role of behaviour in the spread of an alien avian species. The species underwent multiple introductions into Australia, and multiple

translocations within Australia, over the course of the XIX and XX centuries, each one of which has generated a leading edge of an invasion wave (Ewart et al. 2018). Common mynas are now one of most common birds in urban centers of the East coast of Australia (Parsons et al. 2006; Sol et al. 2012) and continue to spread westward (Atlas of Living Australia website <http://www.ala.org.au>) following published climate-matching predictions (Martin 1996). Here, we compared birds from the front and source of an invasion gradient extending westward from the coastal city of Newcastle to begin identifying whether behaviour, and if so which ones, might be underpinning the range expansion of mynas in New South Wales (NSW).

We hypothesized that neophobia would be involved in the range expansion of common mynas. Neophobia (also referred to as ‘risk-taking’ or ‘boldness’; Réale et al. 2007) refers to the avoidance of novelty (Greenberg 2003) and is often studied in birds by measuring the latency to forage in the presence of a novel object (Greenberg & Mettke-Hofmann 2001; Griffin & Guez 2014). When colonizing yet unoccupied geographic areas, birds might encounter new habitats and have to deal with novel resources. Consequently, one might expect a greater willingness to interact with novelty, or at least a reduced tendency to avoid it, to be functionally adaptive. In support of this prediction, invasion front sparrows are less neophobic and more exploratory than long-established invasion source sparrows (Martin 2005).

It has been shown multiple times that neophobia is consistent across time and contexts in mynas (Griffin et al. 2013; Lermite et al. 2017), suggesting the trait has a heritable component. Based on this and prior work in house sparrows, we had reason to hypothesize that neophobia is involved in the range expansion of common mynas and that we should find a front-source difference in this trait. The direction of the expected difference was more difficult to predict, however. In the case of the common myna, the

invasion is moving westward from large cities on the east coast to smaller inland urban centres, which constitute built-up areas separated by large expanses of rural habitat (www.feralscan.org.au/mynascan/). Given that one urban centre might be quite similar to another urban centre, it is not self-evident that reduced neophobia is adaptive on the leading edge of this myna invasion wave, unlike sparrows. On the other hand, lowered responses to novelty might be associated with range expansion because front mynas have presumably had to transit (or descend from birds that recently transited) through expanses of unfamiliar agricultural habitat to reach new urban areas. Other considerations suggest rather that responses to novelty should be higher in front mynas. Indeed, previous research in our group has shown that mynas from sub-urban areas display higher levels of neophobia than birds living in the city centre (Sol et al. 2011). Given that front townships tend to be smaller, more rural urban developments, colonizing front areas might be associated with the same heightened neophobia found in suburban mynas (Sol et al. 2011). Hence, given the difficulty of generating an a priori prediction regarding the expected direction of a population difference (Fig 1), we withheld from making a prediction as to the direction of the predicted difference.

We predicted that there would be a difference in sociality across the invasion front and source. The involvement of sociality in the spread phase of the invasion process has been predicted by other authors on the basis that low tolerance of conspecifics should hasten dispersal from high density to low density populations (reviewed in Chapple and Wong 2016). Support for this hypothesis has been found in invasive lizards and mosquitofishes whereby less social individuals show a higher tendency to disperse suggesting personality-biased dispersal towards the invasion front (Cote & Clobert 2007; Cote et al. 2010). The common myna is a highly social bird species. Individuals mate for life and both parents care for offspring. Juvenile mynas

(following natal dispersal), male mynas (all year round), and almost all adult and year-hatch birds (in winter) overnight in communal roosts (Counsilman 1973). Roosts can contain more than 1000 individuals (Old et al. 2014).

The high sociality of mynas is consolidated by a heavy reliance on social learning, which is central to the high behavioural flexibility of the species (Griffin 2004; Griffin 2008). Based on these clear social tendencies, it seemed reasonable to hypothesize that less social individuals, perhaps those less reliant upon social learning, might have a higher tendency to leave populated source areas and move towards less densely populated front ones. By extension, front mynas should present lower sociality relative to source mynas. Because the temporal and contextual consistency of individual variation in sociality has not been tested before in mynas, we also measured sociality across two different contexts. That is, we measured mynas' responses to two different social stimuli: a mirror and a pair of conspecifics.

In a majority of taxa, the decision to disperse often occurs shortly after behavioural independence from parents, either just afterwards, as in natal dispersal, or when seeking to establish a first breeding territory (pre-breeding dispersal) (Matthysen 2012). In birds, juveniles disperse most often in view of establishing a first breeding territory (Lebreton et al. 2003; Votier et al. 2008; Bicknell et al. 2014). In adults, once individuals have established a successful breeding territory, birds tend to return each year to the same nest (Darley et al. 1977; Gratto et al. 1985; Reed and Oring 1993; Haas 1998). Juvenile mynas, distinguishable from adults on the basis of their brown plumage, move from their natal territory to communal roosts shortly after fledging, and breeding dispersal is thought to be undertaken by hatch-year birds shortly before, during or after, winter (i.e. the non-breeding season). Common mynas on established breeding territories are reported to return to the same territory year after year (Markula et al.

2009; Peneaux and Griffin 2016). Therefore, we expected that any behavioural differences between front and source birds would be strongest at the point in an individual's lifetime when the motivation to disperse is presumed to be highest, that is, in juvenile birds. Hence, we focused our behavioural sampling on this age category.

The aim of this study was to test the hypothesis that sociality and risk-taking play a role in the range expansion of the common myna. This was done by comparing the behaviour of mynas from long-established (source) and recently-established (front) populations. While we predicted that mynas at the front would be less social, and display different levels of neophobia (risk-taking), than mynas at the front, we made no directional prediction with regards to neophobia. Finally, increased tolerance of humans, is consistently associated with birds that live in cities. For this reason, we also compared responses to human disturbance in order to begin disentangling whether front/source differences in neophobia were a signature of personality-dependent dispersal (via habitat matching) or of a plastic response to front habitats.

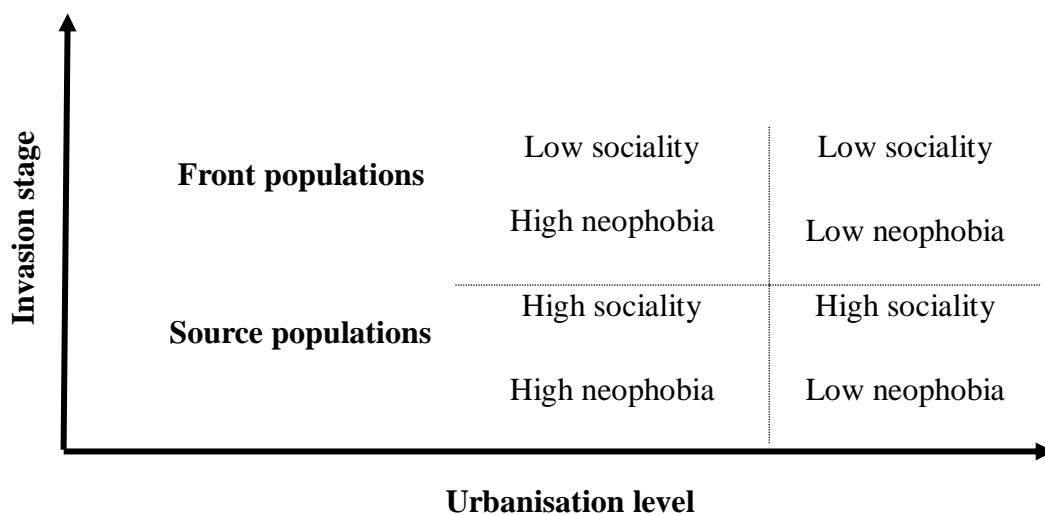


Figure 1. Adaptation of the Two-Factor model on neophobia proposed by Greenberg & Mettke-Hoffmann 2008 to describe potential level of sociality and neophobia as a function of the degree of urbanisation and the stage of the invasion in common myna populations.

Methods

1. Myna trapping, husbandry and captive procedures

We captured forty-nine juvenile common mynas across five locations in New South Wales, Australia, using a walk-in baited trap specifically designed to trap this species (Tidemann 2005). All trapping took place in the backyard gardens of residential buildings. The trap consists of two cages placed one on top of the other. Birds access the bottom cage from outside through two openings baited with dog pellets and then enter the top cage where they can roost on perches through two one-way channels (see Griffin 2008 for details). Although we used one invasion wave as is standard practice in invasion biology research to date (Llewelyn et al. 2010; Gruber et al. 2017), several locations were sampled within that invasion wave. Fifteen mynas (9 females and 6 males) from long-established source populations were trapped in three locations within the larger Newcastle area, where mynas are reported to have been breeding since the 1970s (Morris 1975; Hone 1976). Thirty-four mynas from the NSW invasion front (21 females and 13 males) were captured in two locations 40 km apart within the Hunter Valley, namely Gloucester and Krambach, where mynas have only been breeding for the last ten years (Atlas of Living Australia website at <http://www.ala.org.au>). We attempted to match the habitat of all selected trapping sites as closely as possible. This was more feasible at the local spatial scale (<1 km) than at the large spatial scale (> few km). This is because trapping sites on the invasion front are necessarily in small western townships surrounded by rural land, whereas trapping sites in long-established areas are in larger coastal cities (i.e. due to the range expansion patterns of mynas from coastal (large) to inland (small) towns).

Trapped birds were transported by car in small individual cotton bags to the Central Animal House at the University of Newcastle, to be weighed, measured (tarsus,

beak and wing) and individually marked with coloured plastic leg bands and a numbered metal band. Juveniles were identified based on their brown plumage and black markings on their cover feathers (Counsilman 1971). Although males are on average heavier than females, the sexes are not distinguishable on the basis of plumage and their weight distributions overlap particularly in juveniles. Thus, to sex mynas with certainty a feather was collected from each bird so that it could be sent it to a commercially available company to obtain a DNA-determined sex (<https://dnasolutions.com.au/>). Birds were released into large outdoor flight aviaries (1.95 m x 2.2 m x 1.0 m) with food (dog pellets) and water ad libitum and left undisturbed for a minimum of seven days to acclimatize to captivity before testing began. During this time, they were treated for coccidian infections by adding a coccidiostat to their drinking water for 10 days. Birds from invasion front populations and invasion source populations were held in spatially separated aviaries.

In order to investigate an individual response to novelty, birds were moved from group housing to individual outdoor aviaries (1.95 m x 2.2 m x 1.0 m) for three days (two days of acclimatization, one day of testing). The aviaries, each one holding a single bird, were positioned in a 15-m diameter circle to allow acoustic and distant visual contact but were far enough apart to ensure that no social learning during tests was possible. Each aviary was equipped with tree branches, perches, a nest box, a water bath, and food and water dishes. In order to quantify each bird's level of sociality, the birds were then moved into individual indoor cages (0.5 m x 0.5 m x 0.6 m) for five days (two days of acclimatization, two days of testing separated by a day of rest). We fitted each cage holding a single bird with perches and a nest box. Birds were provided with ad libitum access to water and food throughout the testing period except for one night of food deprivation prior to measuring the birds' response to novelty. All

procedures and protocols were approved by the University of Newcastle Animal Care and Ethics Committee (Animal Research Authority n° A-2014-424).

2. Behavioural testing procedures

2.1 Neophobia

Each bird's response to novelty (neophobia) was measured using a standard protocol widely used in avian research (Greenberg 2003, Jolles et al., 2013, Greggor et al 2016, Lermite et al 2017, Griffin & Guez 2015). Briefly, the rationale of the test is to compare an individual's latency to begin feeding from a familiar food dish in the absence versus the presence of a novel object. In the standard protocol (reviewed by Griffin & Guez 2015), birds are food-deprived prior to testing and the test without the novel object is followed immediately by the test with the novel object. In this way, the test without the object provides a measure of an individual's baseline feeding motivation. Individuals are watched for a set, maximum amount of time when the novel object is present and those that fail to feed are allocated a maximum feeding latency. The delay to feeding caused by the presence of the novel object relative to the delay when the object is not present is considered to provide a measure of fear of novelty.

We have shown previously that responses to novelty are highly repeatable in common mynas across objects, time and contexts (Griffin et al. 2014; Lermite et al. 2017). Nevertheless, to ensure once again that neophobia was object-independent, each bird underwent one test without a novel object followed immediately by *two* successive novel object tests, each one with a different object. The two different objects were ones mynas are unlikely to encounter in the wild, namely a green plastic hairbrush and a pink doorstop. The presentation order of the two novel objects was counterbalanced across birds.

On the evening before the test, each bird's familiar food dish was removed shortly before nightfall. Early next morning, the experimenter approached the aviary from behind a hide and placed a dog pellet in the focal myna's familiar food dish, before returning to the hide. Latency to consume the food item was then measured starting from when the food item had been placed in the dish. We considered this latency to feed to be a measure of the individual response to human disturbance as has been the case by previous authors (Overington et al. 2011; Audet et al. 2015; Ducatez et al. 2016). The test was aborted and the dog pellet removed if the focal myna failed to consume the food within 30 min. The test was then initiated once again an hour later when the individual was assumed to be slightly hungrier. Immediately after the bird had consumed the food, the experimenter approached the aviary a second time and placed a dog pellet in the dish and a novel object next to the dish before returning to the hide. Latency to consume the food item was measured once again and was capped at 1800 s (30 min). As soon as the bird had consumed the dog pellet or at the end of the 30-min time period, whichever occurred sooner, the experimenter approached the aviary a third time, placed a new dog pellet in the bird's food dish (if the previous one had been eaten) and then replaced the first novel object with the second one before returning to the hide. Latency to consume the food item was measured once again, and was again capped at 1800 s. At the end of testing, all objects were removed and the focal bird was placed back on ad libitum food. Within 24 h of completing the neophobia procedure, each bird was moved to an indoor individual cage and left undisturbed for two days before undergoing the sociality tests.

2.2 Sociality

We conducted two separate tests to quantify each bird's level of sociality across two different contexts. Both tests are commonly used in the avian literature (Gallup 1968, Svendsen & Armitage 1973, Kaidanovich-Beilin et al 2011). In the first test, sometimes referred to as a 'self-recognition' test (Gallup 1970; Shillito et al. 1999) or as a mirror-image stimulation test (Kusayama et al. 2000), we quantified each bird's tendency to respond to its own reflection. Each bird's home cage was wheeled into a room (2.8 x 1.7 x 2.7 m) adjacent to the room where the home cages were located. The cage was placed next to a mirror (0.5 m x 0.4 m x 1.1 m), which was covered with a dark cloth. The bird was then left alone for 10 min to acclimatise to its new visual surroundings. Then, its behaviour was recorded using a camcorder for 5 min. This time period provided a baseline period against which its response to its reflection could be compared. The mirror was then revealed remotely by pulling a string attached to the cloth and the response of the bird to its reflection was recorded for a further 5 min. At the end of the second 5-min period, the bird's home cage was wheeled back into the holding room.

Forty-eight hours later, birds underwent a second sociality test. Here, we quantified the bird's tendency to aggregate with two live unfamiliar conspecifics. To begin the test, the focal bird was confined in its nest box and its home cage wheeled into the same room where the previous sociality test had been conducted. The home cage was positioned between two other cages, which were identical to the one in which the focal bird was held. One of these two additional cages was empty. The other one held two conspecific mynas, which were not visible because their cage was covered with a black cloth. The two conspecifics were either of the same sex (either male or female) or of opposite sexes and were unfamiliar to the focal birds (held in different aviaries before the tests). After a few minutes, the cloth was removed and the nest box opened allowing

the focal bird to exit. The experimenter then left the room and the focal bird was videorecorded for 60 mins. At the end of the test, the focal bird's cage was wheeled back into the holding room.

The position of the empty and conspecific cages was counterbalanced across birds in order to ensure that positional preferences of the focal bird were not the result of some underlying factor (e.g. proximity to the room's door). The two conspecific birds that acted as social stimuli remained in their cage for the time needed to test five focal mynas in a row and were then swapped for another pair. This approach provided the opportunity to replicate the experiment with different social conspecifics, while also limiting the possibility that moving the conspecifics in and out of cages caused arousal responses that might have affected the way the focal birds responded to them.

3. Data Analysis

In order to test the repeatability of individual latencies to feed in the presence of the two different novel objects (see above), we calculated an intraclass correlation coefficient (Lessells & Boag 1987). In order to compare neophobia levels across front and source mynas, we fitted a Cox mixed regression model to the feeding latencies using the R package *coxme* (Therneau 2015). The Cox regression, a form of survival analysis, is used to model time to an event (often death) data, in which latencies for the event to occur are recorded and capped latencies result from cases in which the event did not occur (e.g. a subject did not die). In the present case, feeding was the event of interest and the latency to feed in the presence of a novel object was the dependent variable. We were thus able to take into account that the feeding latencies included capped time values for those individuals that did not feed next to the novel object within the maximum amount of time we allowed them. This Cox regression in its mixed form requires few assumptions and allows the inclusion of covariates and random factors in

the one model (Crawley 2002). The inclusion of random factors allowed us to account for the repeated structure of the dependent variable (two objects per individual). Invasion stage (front vs source), sex, and trial (first trial versus second trial) were entered into the survival model as categorical predictors. Latency to feed without an object was entered as a continuous covariate. Two interactions (invasion stage by trial and invasion stage by latency to feed without object) were also included in the model, and birdID (individual) was entered as random factor. Then, to test whether mynas from the two populations differed in their levels of human tolerance, we ran a second cox regression model using the latency to return to feed in the absence of a novel object. Because this latency is collected by a human approaching the bird and providing only a food item (no novel object), the latency is often used as a measure of responsiveness to human disturbance (Ducatez et al. 2016). Invasion stage (front vs source) and sex were entered into the survival model as categorical predictors. The interaction between the two factors was entered in the model (invasion stage by sex) and birdID (individual) was entered as random factor.

For both the self-reflection and the live conspecific test, we divided the focal bird's cage into three equally sized zones. Zone 1 encompassed the area closest to the social stimulus (mirror or social companions), zone 2 encompassed the middle of the focal bird's cage, and zone 3 encompassed the area furthest from the social stimulus. The common assumption in this test is that a bird's positioning relative to a conspecific reflects its motivation to approach versus avoid it, i.e. its level of sociality (Faure and Mills 2014), so we modelled time spent in zone 1 in both tests. To obtain an additional measure of sociality during the self-reflection test, we scored behaviour from the 10-min video-recordings of each focal bird (5-min without mirror, 5-min with mirror), counting the number of movements (including all flights and walks) and the number of

social calls produced both before and after the birds were exposed to their reflection in the mirror. To measure each bird's social response to the two live conspecifics, we scored each focal bird's 60-min video recording, counting the number of movements. Contrary to the self-reflection test, it was not possible to count the number of social calls because it was not possible to ascertain whether the recorded calls were produced by the focal bird or by the conspecifics.

We analysed these variables (time spent in zone1, number of movements and number of social calls) using GLMM models, R package lme4 (Bates et al. 2014). We applied Poisson or negative binomial error distributions, after checking the residuals' over-dispersion coefficients to ensure optimal fit (Bolker et al. 2009). For the self-reflection test, Time in zone1, number of movements and number of social calls were modelled including invasion stage (source versus front), sex, test phase (5-min without mirror, 5-min with mirror) and the interaction between invasion stage and test phase, while bird ID was fitted as a random factor. For the proximity test, Time in zone1 and number of movements were modelled including invasion stage (source versus front), focal bird sex, demonstrator sexes (MF, MM, FF) and the interaction between invasion stage and sex, while bird ID was fitted as a random factor.

All tests were carried out using SPSS 24 (SPSS Inc., Chicago, IL, U.S.A.) and R v3.4.3 (2017). Two-tailed tests were used throughout and alpha levels were set at 0.05.

Results

Neophobia in source vs. front populations

The neophobic response was consistent across the two novel objects (intraclass correlation coefficient $r = 0.665$, $P < 0.0001$) (Lessells et al. 1987). The survival

analysis revealed that invasion stage (front vs. source) predicted the level of neophobia (Table 1). Front birds were significantly more neophobic than birds from the source (Fig 2). The latency to feed in the absence of an object was also a significant predictor of the latency to feed in the presence of a novel object, whereby birds that fed more quickly in the absence of a novel object also fed more quickly in the presence of novelty (Table 1). In contrast, the interaction between the latency to feed in the absence of an object and the invasion stage was non-significant (Table 1, Fig 2), implying that the slope of the relationship between latency to feed in the absence and the presence of an object did not differ between front and source mynas. Neither invasion stage, nor sex of the focal individual influenced the time to return to feed after a human disturbance in the absence of object (Table 2, Fig 2).

Table 1. Risk-taking in juvenile common mynas. Cox regression model on the latency to feed in the presence of a novel object (neophobia).

<i>Fixed effects</i>	coef	exp(coef)	se(coef)	Z	P
Invasion stage (source)	1.888	6.612	0.575	3.28	0.001**
Trial (Trial 2)	0.101	1.107	0.199	0.51	0.610
Latency to feed in the absence of object	-0.001	0.998	0.0006	-1.98	0.048*
Sex (male)	0.492	1.635	0.356	1.38	0.170
Invasion stage~trial	-0.033	0.966	0.356	-0.09	0.920
Invasion stage~Latency to feed in the absence of object	-0.001	0.998	0.001	1.03	0.300
<i>Random effect</i>	Sdt Dev	Variance			
BirdID	0.914	0.835			

The reference category of each variable is noted in brackets. * P<0.05; **P<0.01

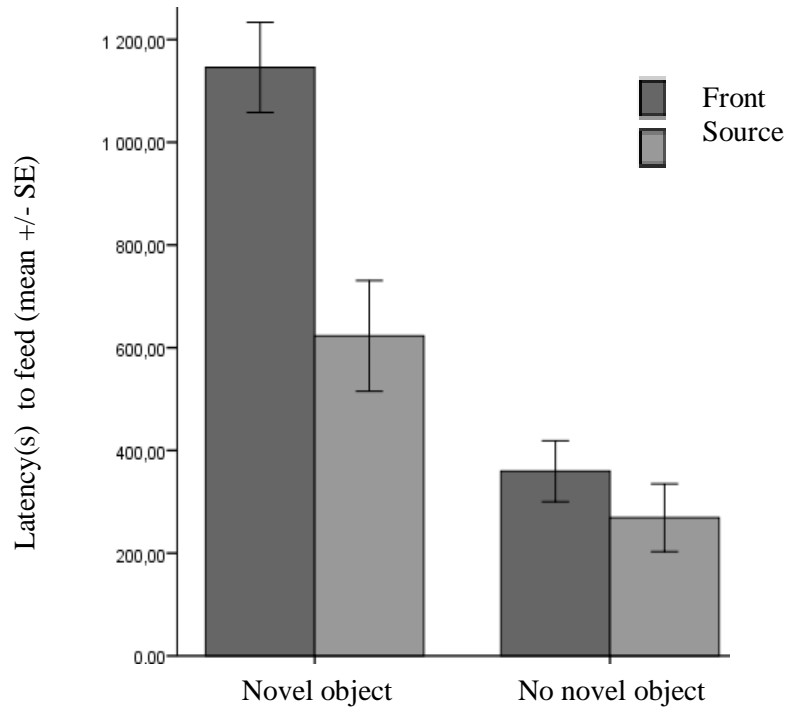


Figure 2. Risk-taking in front and source juvenile common mynas. Latency to feed in presence and in the absence of a novel object as a function of invasion stage.

Table 2. Responsiveness to human disturbance in juvenile common mynas. Cox regression model on the latency to feed in the absence of a novel object.

<i>Fixed effects</i>	coef	exp(coef)	se(coef)	Z	P
Invasion stage (source)	0.238	1.269	0.425	0.56	0.57
Sex (male)	-0.542	0.581	0.926	-0.59	0.56
Invasion stage~sex	0.415	1.515	0.6627	0.63	0.53
<i>Random effect</i>	Sdt	Variance			
	Dev				
BirdID	0.019	0.0003			

The reference category of each variable is noted in brackets. *See text for more details.*

Sociality in source vs front birds.

In the self-reflection test, both source and front mynas showed an approach response to the social stimulus, i.e., their self-reflection, spending significantly more time in the zone closest to the mirror after it had been revealed than beforehand (Table 3, Fig 3a). However, we found no evidence of significant differences in the time spent closest to the social stimulus between birds of different sexes or invasion stages (Table 3). Similarly, the models on the number of movements or social calls during the two phases of the test did not show significant differences between sexes or between front and source mynas (Table 3, Fig 3b and c).

Table 3. Sociality in front and source juvenile common mynas measured using a mirror test. GLMM (negative binomial error, log link) on factors affecting mynas' responses to their self-reflection

Dependent variable	Independent variable	Estimate	Std. Error	Z	P
Time spent close to social stimulus	Invasion stage (source)	-0.5087	0.4756	-1.07	0.28
	Test phases	1.3325	0.3720	3.58	<0.001**
	Sex (male)	0.0105	0.4522	0.02	0.98
	Invasion stage ~ Test phases	-0.0126	0.6738	-0.02	0.98
Activity	Invasion stage (source)	-0.3774	0.3106	-1.22	0.22
	Test phases	-0.2674	0.2448	-1.09	0.27
	Sex (male)	0.1476	0.2968	0.50	0.62
	Invasion stage~ Test phases	0.0413	0.4431	0.09	0.93
Vocalizations	Invasion stage (source)	-5.865	42.058	-0.14	0.89
	Test phases	0.556	0.501	1.11	0.27
	Sex (male)	0.555	0.839	0.66	0.51
	Invasion stage~ Test phases	9.020	59.474	0.15	0.88

The reference category of each variable is noted in brackets. Bird ID (individual) was entered as a random factor. * P<0.05; **P<0.01 Test phase refers to each of the two 5-min parts of the test: mirror covered and then mirror revealed.

Neither invasion stage, nor sex of the focal individual, nor the composition of the pair of demonstrators influenced the time spent close to the pair of conspecifics or the number of movements exhibited by the focal bird in the proximity test (Table 4).

Table 4. Sociality in front and source juvenile common mynas measured using a proximity test. Results of GLMM testing the factors that influence mynas' social responses to a pair of live conspecifics.

Dependent variable	Independent variables	Estimate	Std. Error	Z	P
Time spent close to the social stimulus	Invasion stage	0.255	0.164	1.55	0.121
	Sex (males)	-0.057	0.143	-0.40	0.690
	Demonstrators (MF)	-0.066	0.154	-0.43	0.66
	Demonstrators (MM)	-0.101	0.171	-0.59	0.554
	Invasion stage~ Sex	-0.019	0.266	-0.07	0.942
Activity (number of movements)	Invasion stage (source)	-0.460	0.260	-	0.077
				1.768	
	Sex (males)	0.037	0.226	0.165	0.869
	Demonstrators (MF)	-0.286	0.243	-	0.239
				1.175	
	Demonstrators (MM)	0.176	0.271	0.649	0.516
	Invasion stage~ Sex	0.642	0.420	1.527	0.126

Reference categories of categorical variables are noted between brackets beside the variable name. Demonstrators: MF refers to male-female pairs, MM refers to a male-male pairs. Bird ID (individual) was entered as random factor. GLMMS applied a Poisson error distribution and a log-link function

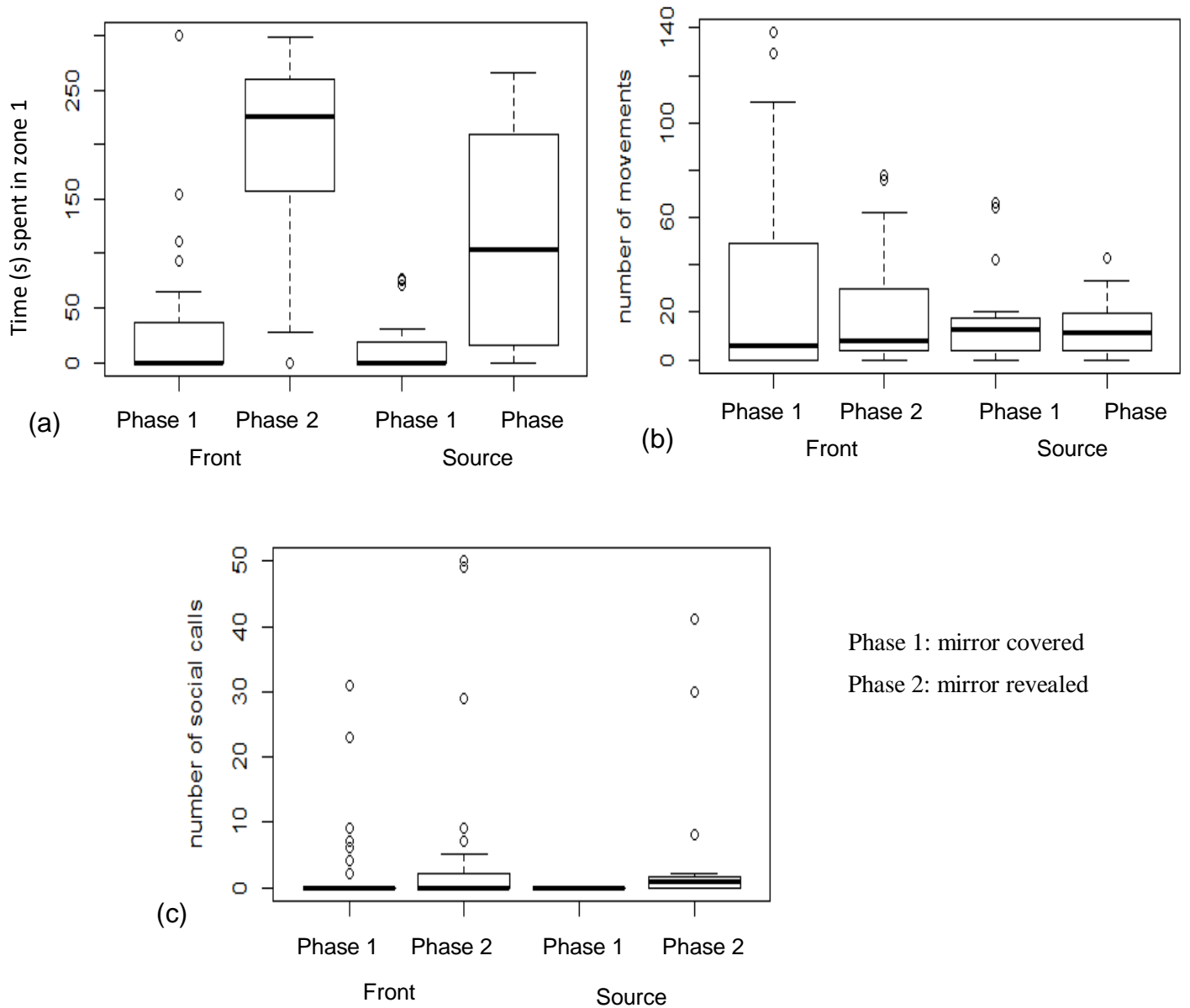


Figure 3: Sociality in front and source populations of juvenile common mynas. The graphs depict boxplots of different dependent variables of the self-reflection test (a) time spent (in seconds) in zone 1 (closest to mirror), (b) number of movements, (c) number of social calls. The line within each box represents the median value, the upper and lower borders of each box are the 25th and 75th percentiles, the lower and upper bars are the 10th and 90th percentiles and circles the outliers.

Discussion

We measured levels of neophobia and sociality in juvenile common mynas from the recently-established western front of the New South Wales (NSW) myna invasion wave and compared these birds' levels with those of juvenile mynas from the, long-established, coastal source of the NSW invasion wave. Juvenile common mynas from the invasion front were significantly more neophobic than juvenile mynas from the invasion source but showed no difference in responsiveness to human disturbance. We found no evidence for our prediction that juvenile mynas from the invasion front were less social than those from the invasion source. The finding that mynas at different stages of the invasion differ in neophobia, but not sociality, provides the first line of evidence that personality-dependent dispersal according to inter-individual variation in neophobia are involved in the ongoing range expansion of common mynas across the East coast of Australia.

Directional predictions on potential differences in levels of neophobia between populations are difficult to make in an invasion context. Since boldness (low neophobia) is often correlated with dispersal (Cote et al. 2010; Fraser et al. 2001; Rehage & Sih 2004), bolder individuals should be found on the front of the invasion. When invading previously uncolonized areas, being bolder could offer some advantage. Shy animals usually spend more time in shelters while bold individuals develop a higher foraging success (Short and Petren 2008). On the other hand, displaying a risky behaviour could be very detrimental when individuals show inappropriate antipredator behaviour for example (Conrad et al. 2011). Different levels of neophobia in front and source populations can be a function of the invasion stage. However, it is also possible that neophobia levels of invasion front individuals not to be a function of the novelty of the

recipient environment *per se*, but rather to be a function of the recipient environment habitat's characteristics. For example, boldness has been associated with survival in urbanised areas where predation pressure appears to be relaxed, but boldness might be disadvantageous in more natural habitat where predation pressure is higher (Short and Petren 2008). Some studies have already explored potential differences in boldness within a species at different stages of the invasion and report very diverse results across taxa (see Chapple et al. 2012; Hudina et al. 2014 for review).

One feature of the ongoing invasion of common mynas across the NSW east coast of Australia is that mynas are spreading from highly urbanized coastal strip westward towards smaller, more rural-based townships (www.feralscan.org.au/mynascan). All birds captured for this study were trapped within comparable front and source urban environments *at the local scale*. At a larger scale, however, these front townships are smaller and are surrounded by rural landscapes. The present finding that front juvenile mynas were more neophobic than source juvenile mynas is consistent with prior work comparing common mynas from urban and suburban habitats; suburban birds were found to be more neophobic than urban ones (Sol et al. 2011). Levels of neophobia could follow a gradient of urbanization along common myna invading range leading to an adaptive habitat matching as a function of the level of urbanisation. Two models could explain these differences in neophobia. On one hand, inter-individual variation on this trait could exist prior dispersal and only the more neophobic individuals range expand producing a higher level of neophobia on the edge of the invasion wave. On the other hand, dispersal could be random with respect to inter-individual variation in neophobia and the difference found in front populations is a consequence of a recent (i.e. within the last decade) genetic or plastic changes in common mynas due to the colonization of less urbanised habitats. Therefore,

populations may vary in their behavior as a function of time, here the level of neophobia could increase as a function of time spent in the novel habitat on the front of the invasion.

We argue that the first explanation, namely that range expansion is non random relative to variation in neophobia is more likely. First, previous work in mynas has demonstrated repeatedly that neophobia is consistent across time and contexts (Griffin et al. 2013; Lermite et al. 2017). This finding is generally taken to indicate that neophobia forms a personality trait with a heritable component, rather than a plastic response to the immediate environment. Indeed, consistency across time and context, described as personalities or behavioural syndromes (Sih et al. 2004), have a genetic basis (Dingemanse et al. 2002; van Oers et al. 2004; Both et al. 2005). Second, common mynas on the front of invasion only differed from source birds in their response to novel objects, but not in their response to human disturbance. Investigations of human tolerance along a gradient of urbanisation in birds have shown consistently that non-urban birds, including mynas, are less tolerant of human disturbance than urban ones (e.g. Crisp & Lill 2006; Møller 2008; Moller et al. 2015; Møller et al. 2015). Together with the present findings, one would need to conclude that front common mynas displayed a ‘rural’ level of neophobia and an ‘urban’ level of tolerance to humans. It is more parsimonious to conclude that differences are the result personality-dependent dispersal along variation in neophobia rather than the result of a plastic response to front environments post colonisation. Future research is needed to investigate additional front/source population replicates to disentangle both influences of the stage of the invasion and the habitat. However those comparisons would be limited to rural front and source populations or rural vs urban source since the pattern of the myna range expansion from the highly urbanised eastern seaboard westward towards more rural

townships does not offer highly urbanized environments on the front of the invasion. Comparisons between rural front and source mynas would help to disentangle the potentially joint effects of habitat and stage of the invasion. For example, if both rural birds at the two ends of the invasion present the same level of high neophobia; one could argue in favour of personality-dependent dispersal and habitat matching. On the other hand, if rural source birds present a lower level of neophobia than front birds; one could argue in favour of invasion stage.

In experimental studies of mosquitofish, Cote et al (2010, 2011) demonstrated that less social individuals showed a higher tendency to disperse and stated the hypothesis that this propensity will provoke a personality bias at the front of the invasion wave. On the contrary, cane toads from invasion front populations presented an increased social attraction in comparison to their counterparts in long-established populations (Gruber et al. 2017) . Other work has failed to replicate this pattern of variation in sociality across invasion waves. For example, the killer shrimp (*Dikerogammarus villosus*) does not present any behavioural difference in sociality as the function invasion stage (Truhlar and Aldridge 2015b). In the present study, across two separate tests of social tendency, juvenile common mynas failed to display differences in sociality between source and front populations. Common mynas are well-known for being gregarious, they often forage in groups and overnight in large communal roosts (Counsilman 1973; Tindall et al. 2007). In addition, common mynas respond strongly to conspecific alarm calls and use them to acquire information about novel food sources (personal observation) and novel predation threats (Griffin 2008). Therefore, it is possible that in a species with such a significant reliance on social information, any decrease in sociality would be detrimental, particularly when colonizing unfamiliar environments.

This study established for the first time that mynas at different stages of an invasion wave show variation in behaviour, and specifically, in their responses to novelty. Whether intra-individual variation in neophobia across the invasion wave is the result of plastic adjustments to local habitats post-settlement, or whether such variation is a driver of spread of mynas across habitats of varying levels of urbanization will require future work. However, it is argued here that more neophobic individuals might be more inclined to colonize less urban environments at the periphery of larger cities, and/or disperse to more distant rural townships as densities increase or in response to the aggressive behaviour of native species (see chapter 4). These findings strengthen the proposition that the study of behaviour is valuable in our understanding of biological invasions.

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Chapter 3.

Invasive versus native bird breeding success in cities: Does good parenting help?

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Abstract

When native cavity nesting birds begin utilizing nesting opportunities in cities in response to large-scale deforestation, they often have to compete with alien cavity nesters. An important factor shaping breeding success is parental care. Yet the role of parental care in shaping the relative breeding success of synanthropic alien and native birds has been largely overlooked. The degree of parental care might be particularly important in cities where cavities suitable for nesting are becoming increasingly rare. Here, we compared the breeding success and parental care of one of the most common alien birds, the common myna (*Acridotheres tristis*), with the breeding success and parental care of native parrots that share the same urban environment in New South Wales, Australia. Using 174 experimental nest boxes in five locations, we compared the breeding success, clutch size and causes of nest failure in mynas and native parrots. Invasive mynas had a reproductive success twice as high as native parrots. By examining parental nest attendance and nest intrusions in a subset of nests, we discovered that native and invasive species showed significant differences in the patterns of parental care. Common mynas were four times more present at their nest

than native parrots and experienced significantly less nest disturbance. These findings suggest that variation in parental care strategies might help explain why invasive mynas higher fledgling success in our cities have than native parrots despite occupying identical nesting structures and laying more eggs per clutch.

Key words: invasive and native species, parental care, nest attendance, breeding success.

Introduction

Habitat loss is recognised as the first and the main threat to biodiversity, just followed by invasive species introduction (Wilcove et al. 1998; Bellard et al. 2016). Habitat destruction results from human population extensions and activities, deforestation for example and its subsequent urban or agricultural developments alter drastically natural habitats (Ehrlich 1988; Wilson 1992). Australia has one of the highest rates of land clearing of all developed nations. Australia has lost nearly 40% of its forests since the first large expansion of European settlements in the late 18th century. This ongoing deforestation has led to fragmented remnant native vegetation (Bradshaw 2012) and a loss of habitat that is particularly detrimental to those species that need trees for shelter, foraging and/or nesting (Gibbons et al. 2008; Lindenmayer et al. 2009). This is a major issue for cavity nesting birds and Australia is home to the highest number of cavity nesting birds in the world. Moreover, no cavity-excavating vertebrate species, such as the woodpeckers, are present in Australia to regularly create new cavities (Gibbons & Lindenmayer 2002). Since cavity formation is therefore based on long processes of invertebrate- and fungus-assisted decomposition occurring mainly in large aged trees (Luck and Smallbone 2010), a delay of several centuries is required before the

formation of resources that could be available for cavity-nesters. Under these conditions, efforts to compensate habitat loss through planting of young trees does not re-establish a sufficient number of hollows once old-growth forests are cleared (Gibbons et al. 2008, 2002). Furthermore, tree-hollow bearing trees are being increasingly removed in urban areas owing to safety concerns (Harper et al. 2005; Morton 2013). Nesting cavities are hence likely to be a limiting resource for native cavity-nesting birds in urban habitats.

Densities of urban-dwelling birds can reach on average 30 times those of non-urban habitats like black-headed gulls (*Larus ridibundus*) in Finland, and as much as 100 times higher for some species such as tree sparrows (*Passer montanus*) in Denmark (Moller et al. 2012). This extraordinary boost in avian population densities within urban areas is thought to be attributable to high supplies of anthropogenic food and low rates of predation (Chace and Walsh 2006; Shochat 2016). It is generally accompanied by a sharp decline in species richness, however, and a sharp increase in the relative proportion of synanthropic alien avian invaders (Marzluff 2001; Mckinney 2006; Kark et al. 2007). High population densities compounded by paucity of natural nesting cavities are likely to make urban habitats very competitive environments for native secondary cavity nesters, particularly in situations where alien species also use cavities for reproduction (Blewett and Marzluff 2005).

Under these circumstances, birds may need to invest more parental behaviours such as nest defence and nest presence to ensure the safety of their cavities and clutches (Cilento and Jones 1999; Evans et al. 2010; Minias 2015; Davies et al. 2016). The nature and percentage of time and energy are shaped by ecological conditions (Clutton-Brock 1991; Bonsall and Klug 2011; Reyes et al. 2016). Assuming that native and alien secondary cavity nesting species have evolved under different conditions, they might

display different patterns of parental care, particularly in cases where they belong to different taxonomic groups. Here, we undertook a study of the potential importance of parental care in explaining differences in clutch success between native and alien secondary cavity nesting avian species on the east coast of Australia.

The common (Indian) myna (*Acridotheres tristis*) is one of the most significant alien invaders globally and in Australia, with whom native Australian secondary cavity nesting parrots must contend in urban areas (Martin 1996; Chace and Walsh 2006; Lowe et al. 2011). As a result of its introduction to Australia mid-19th century, the common myna is now one of the most abundant bird species in many cities along the eastern seaboard (Sol et al. 2012; Haythorpe et al. 2013 Nov 24). The species continues to range expand westward from the coast (Martin 1996). This pattern of ongoing spread creates opportunities to examine how demography and behaviour of native species and common mynas might change as a function of how long mynas have been established. This can be achieved by studying mynas and natives simultaneously in areas where mynas have been established for a long time and areas where mynas have only recently begun breeding (constituting the front of the invasion wave).

While there is evidence that mynas are reproducing at higher rates than native parrots (Grarock et al. 2013), the reasons underpinning the myna's range expansion and success remain unclear. Some have suggested it is at least partly due to its capacity to aggressively outcompete native parrots over limited nesting resources (Pell and Tidemann 1997). However, evidence for such direct aggression remains mixed and conclusions debated. A hypothesis that has not yet been examined is that native parrots and alien common mynas differ in their levels of parental attendance at the nest, which can in turn influence the level of nest intrusions and affect reproductive output in competitive urban environments. Native parrots and common mynas may differ in their

levels of nest attendance for a variety of reasons, including, for example, diet-related differences potentially affecting the rates at which nestlings are fed.

The aims of this study were to examine whether native Australian parrots have different reproductive outputs in urban areas compared with the invasive common myna and to determine whether or not the level of nest attendance and nest disturbance might explain any interspecies variation in reproductive output. We predicted that (1) common mynas would have a higher reproductive success in comparison to native parrots and that this difference would increase as a function of time common myna arrival since (as a function of number of years of competition for nesting cavities); (2) native parrots would spend less time at their nest than the invasive species; (3) native parrots would experience higher rates of disturbance by competitors (other secondary cavity-nesters) and predators than common mynas.

Methods

Study site selection and nest box locations

In order to investigate the breeding success of alien common mynas and native cavity nesting parrots, we selected eight study areas within the common myna invading range using Australian bird records over the past century (McKinney and Kark 2017). In 2014, four study sites were selected in areas where myna breeding has been recorded for over 40 years (long-established sites) and four study sites were selected in areas where myna breeding has only been recorded within the last decade (front sites). To also account for the effect that habitat variation might have breeding success and patterns of

parental care, we placed nest boxes within three distinct types of habitat (sub-environment) within each study site, namely urban, park and bush edge. We matched as closely as possible the three types of habitat within each study site. Since the common myna invasive wave is moving westward from highly urbanised coastal cities to more rural townships where urban habitat subsides more quickly to rural habitat, front source sites were more urbanised at large spatial scales (>5 km). At a local scale (<5 km), however, each of the three habitats were well matched across sites. Boxes were always placed along streets (urban), in urban parks (park) and along the edge of a bushy area (edge of bush) in all front and source study sites.

In total, we installed 174 experimental nest boxes across all study locations; 32 boxes in each habitats on the front of the invasion; 31 boxes in urban and park habitats and 16 in edge habitat in long-established sites (Fig. 1, Appendix 1&2). We used vertical nest boxes made of plywood suitable for native cavity-nesters. Internal dimensions were 400 (H) x 170 (W) x 170 (D) mm and the entrance hole measured 65 mm diameter. This design was informed by former nest box studies examining interactions between common mynas and native parrots (Orchan et al. 2012; Grarock et al. 2013) and consisted of a model specifically designed to suit the avian competitors of native birds of the genus *Platycercus* (Nest Boxes Australia, Loganholme 4129 Australia). Each box was fitted with a 75-cm external perch located approximately 3 cm under the entrance to allow birds to land on the box before entering. An internal ladder was carved out of the nest box internal wall to allow parents and chicks to access the box following Orchan et al (2012).

Nest box occupancy and breeding success monitoring

We monitored all nest boxes on a weekly basis using a gooseneck camera set up on a long PVC pole and connected to a Bluetooth monitor for an entire breeding season (August 2015 to April 2016). During weekly monitoring, we collected information on species ownership but also on number of eggs, nestlings and fledglings. The number of eggs and the number of fledglings recorded for each nest box allowed us to calculate the number of eggs per clutch (egg ratio) for each species and the number of fledglings per individual. The number of fledglings per individual was calculated by dividing the number of fledglings produced by a pair of parents over the entire breeding season by two (i.e. number of chicks surviving divided by 2). For each nest box, we recorded the number of breeding attempts by species, and for each attempt, whether it was successful or not. An attempt was counted each time a pair of birds laid at least one egg in a box. In cases where no egg in a clutch hatched, or none of the nestlings fledged, we recorded a nest failure. Each time we found a box to be empty the week after it had been recorded to contain nestlings very close to fledgling age, we recorded a successful nest.

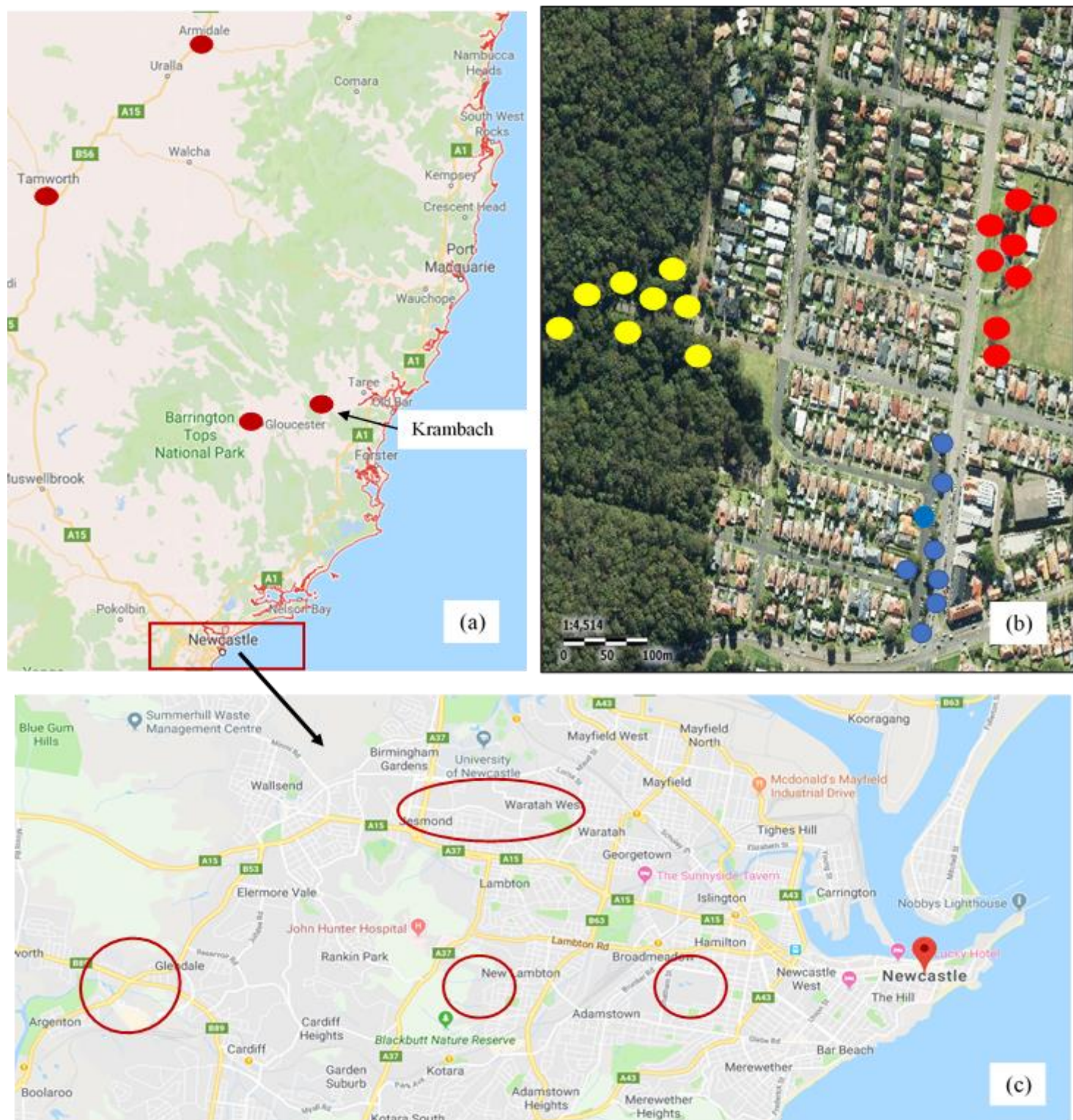


Figure 1 Nest box locations

(a) Study site locations in NSW. Four sites on the front of the common mynas invasion wave (Armidale, Tamworth, Krambach and Gloucester). Four sites in long-established populations of common mynas in the Newcastle area (see (c)). (b) Map of the three sub-environments of one of the source sites (New Lambton, Newcastle). Black dots (urban sub-environment), triangles (park sub-environment) and squares (edge of the bush sub-environment). Each symbol refers to one nest box (24 boxes per site, 8 boxes per sub-environment). (c) Four long-established study sites locations in Newcastle area.

Causes of failure, intrusions and parental nest attendance

In order to gain more precise information on the causes of clutch failure and tease apart those attributable to nest desertion, nest predation, and nest take-over, we installed movement-triggered cameras (Little Acorn surveillance cameras model LTL-5310x – 5) near a subset of occupied nest boxes (n=14, including eight nests of eastern rosellas (*Platycercus eximius*) and six nests of common mynas). The cameras were installed in front of each nest box in order to record all events occurring in the vicinity of the nest. The cameras were set up to capture an image each time a movement occurred around the nest during both day and night, with a 30 seconds interval between two activations. This approach reduced the number of pictures collected by moving branches and leaves, which decreased battery life and consumed considerable memory card space. Each occupied nest box was recorded from the time at which an egg was found to the point in time when all birds had left the nest. Trigger camera images were downloaded weekly from the cameras and batteries were changed in order to ensure ongoing data collection.

The images revealing the presence of animals close to the nest were sorted into four categories depending on which animal was sighted: (1) parents, (2) predators, (3) other secondary cavity nesters, which we refer to as ‘competitors’, (4) all other species, which we refer to as ‘intruders’. All pictures displaying the presence of conspecifics were categorized as parents because it was clear in most cases that the birds were parenting the clutch rather than intruding (rapidly entering and/or exiting the box after landing on the roof or the perch at the nest entrance). For each nest box and each image category, we divided the total number of images captured by the number of days the box was observed (i.e. the camera was functional) to estimate the level of parental nest attendance, as well as visitation levels by intruders, competitors and predators. It is possible and even likely that images resampled the same individual visitor repeatedly,

but this was not a concern because we were interested in overall disturbance levels. So, for example, even if a nest was visited by one individual cat five times or by five different individual cats once each, we considered the level of disturbance to be the same.

For a subset of nest boxes, we were able to cross-compare the patterns of disturbance captured on trigger cameras with patterns of egg and clutch survival obtained during weekly monitoring, which allowed us to identify any causal relationship. We classified failures into several categories: hatch failure, egg predation, and chick death, noting each time whether these events were due to a nest box take-over. We used the term take-over only when we were able to locate both the resident and the intruder species at the same time in the nest box.

All procedures and protocols were approved by the University of Newcastle Animal Care and Ethics Committee (Animal Research Authority n° A-2014-424).

Data Analysis

Native parrots were predominantly represented by eastern rosellas. A maximum of three boxes per season were occupied by other parrot species (crimson rosella, *Platycercus elegans*; rainbow lorikeet, *Trichoglossus moluccanus*). Therefore, we compiled data from different parrot species under the label native parrots for all analyses except that of egg ratios where a visual inspection of data suggested a large difference between rainbow lorikeets and rosellas.

We calculated the percentage of nest box occupancy for common mynas and native parrots. As the distribution of this variable was not normal, we used a non-parametric independent Kruskal-Wallis test to investigate a potential difference in nest

box occupancy across native parrots and common mynas. We used a Generalized Linear Mixed Model (GLMM) with a Poisson distribution and a log link (Lme4 R package, Bates et al. 2014) to examine the effect of invasion stage (source/front), species and sub-environment on breeding success with number of fledglings per individual as the target variable. Nest box ID and study site were entered as random factors. Independent Mann-Whitney tests were used to compare the mean number of eggs/clutch across parrots and mynas

In order to test for differences in parental nest attendance and nest disturbance across species (native parrots versus common mynas) in the subset of nests monitored by trigger cameras, we used non-parametric Independent Samples Mann-Whitney-Wilcoxon tests. We examined whether higher nest attendance was associated with lower levels of nest disturbance using a Pearson correlation. Finally, we used Mann-Whitney tests to test whether parental presence and nest disturbance varied across nests depending on nest outcome (success, failure).

Statistical analyses were carried out using SPSS statistics 22.0 except for the GLMM that was run in R version 3.2.2 (R Core Team 2015). Two-tailed tests were used throughout and alpha levels were fixed at 0.05.

Results

Nest box occupancy

Overall, 30% of the 174 nest boxes were occupied by bird species during the 2015-2016 breeding season. Common mynas were present in 47.2% of occupied boxes and rosellas in 45.3% of occupied boxes (Table 1). Two boxes (3.8%) were occupied by rainbow

lorikeets and two boxes (3.8%) by European Starlings (*Sturnus vulgaris*). Percentages of occupancy by native parrots (rosellas and rainbow lorikeets) were not significantly different to percentages of occupancy by common mynas (Independent Samples Kruskal-Wallis Test $Z=0.001$, $df=1$, $P=0.977$).

Table 1 Nest occupancy and breeding success in common myna and native parrots.

Species	% of occupied boxes	# of attempts	# of success	# of failures	# of eggs	# of fledglings	# of fledglings per individual
Common mynas*	47.1	37	29	8	135	70	1.4
Native parrots**	49	34	12	22	153	32	0.5

* 25 nest boxes occupied by common mynas, ** 24 nest boxes occupied by eastern rosella, 1 by crimson rosella and 2 by rainbow lorikeet. # refers to number

Breeding success

Common mynas fledged significantly more chicks per individual (1.4 ± 0.21 SE) than native parrots (0.5 ± 0.18 SE), Poisson GLMM: $Z=-3.1$, $P=0.001$ (Table 2, Fig 2). The number of fledglings per individual did not differ between long-established and recently established populations or across urban, park and forest edge sub-environments. Therefore, all subsequent analyses were undertaken on data combined across invasion stages and across sub-environments. Common mynas fledged significantly more chicks per breeding attempt than native parrots (Independent Samples Mann-Whitney U-Test: $n_{\text{(myna)}}=25$, $n_{\text{(parrots)}}=27$, $U=168.5$, $P=0.001$), as well as significantly more fledglings per egg laid ($U=145$, $P<0.001$) (Fig 2). These results suggest that Common mynas were more successful than native parrots at every stage of breeding.

Table 2. Generalized linear mixed model of number of fledglings per individual as a function of invasion stage, sub-environment and species (common mynas vs. native parrots). Nest box ID and study site were entered as random factors.

Term	Coefficient	SE	Z	P
Intercept	1.1671	0.4332	2.694	0.007
Species (Native parrots)	-1.1174	0.3553	-3.145	0.001 **
Invasion stage (Source)	0.1321	0.4657	0.284	0.776
Sub-environment (Park)	-0.3568	0.6041	-0.591	0.554
Sub-environment (Urban)	-0.6389	0.4954	-1.290	0.197

Positive coefficients indicate that the variable increases the likelihood of fledgling. Reference categories for categorical explanatory variables are indicated in brackets. SE: standard error. * P<0.05; **P<0.01

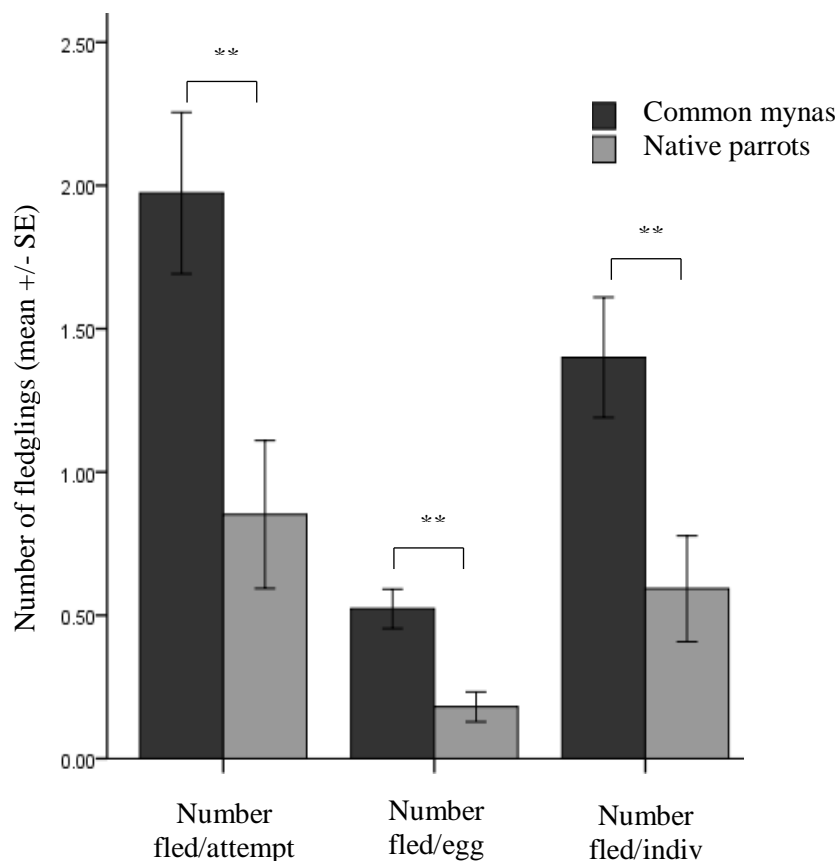


Figure 2. Mean number of fledglings per attempt, per egg and per individual in common mynas and native parrots.

Common mynas laid on average more eggs per clutch (mean egg/clutch 3.6 ± 0.998) compared with the rainbow lorikeets (mean egg/clutch 2 ± 0.00) and fewer eggs than rosellas (mean egg/clutch 4.5 ± 1.41). Independent Samples Mann-Whitney tests revealed that the difference between mynas and rosellas clutch size was significant ($Z = -2.9$, $n_{\text{mynas}} = 37$, $n_{\text{rosella}} = 32$, $P < 0.003^{**}$, Fig. 3). The number of clutches laid by rainbow lorikeets was too small to perform any meaningful statistical analyses.

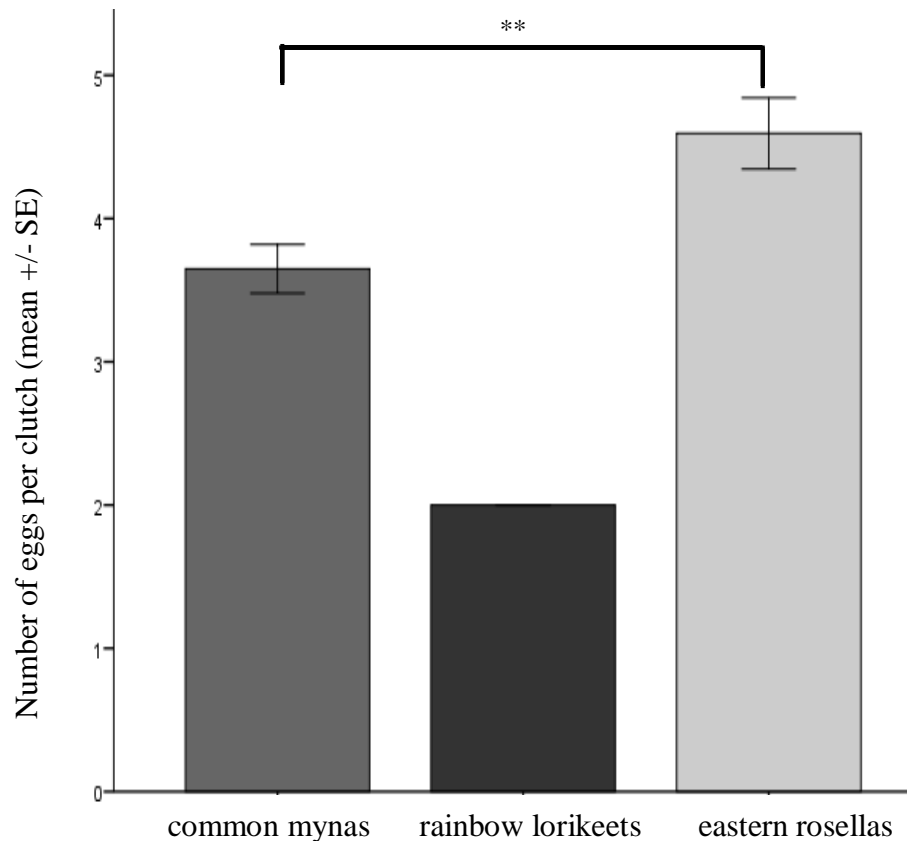


Figure 3. Mean number of eggs per clutch and per species.

Causes of nest failure

Twenty-two parrot clutches (64.7%) (rosellas and rainbow lorikeets) failed whereas only eight common myna clutches (21.6%) failed (Chi-square =11, df=1, $P=0.001$). Statistical analyses revealed that hatch failure was a more common cause of failure in rosellas (50%) than in common mynas (Independent Samples Mann-Whitney U-Test, $n_{\text{(myna)}}=8$, $n_{\text{(parrots)}}=22$, $U=132$, $P=0.04$). In contrast, chick death was a more common cause in common mynas (62.5%) (Independent Samples Mann-Whitney U-Test, $n_{\text{(myna)}}=8$, $n_{\text{(parrots)}}=22$; $U=22$, $P=0.001$). The percentage of egg predation was no different in mynas (37.5%) and native parrots (40.9%) (Independent Samples Mann-Whitney U-Test, $n_{\text{(myna)}}=8$, $n_{\text{(parrots)}}=22$; $U=110$, $P=0.32$). In two breeding attempts, parrot chick death was due to take-over by other species. In one instance, an eastern rosella nest was taken over by a pair of rainbow lorikeets. In a second instance, an eastern rosella nest was taken over by native bees.

Nest disturbance, parental attendance and potential effect on breeding success

One eastern rosella nest was usurped by a pair of rainbow lorikeets across a period of several days and underwent an extremely high level of disturbance (14 times higher than the average of other boxes). As the take-over process took several days, it was impossible to determine exactly when this rosella nest became a rainbow lorikeet nest and consequently to distribute parental attendance and disturbance among each of the species. In addition, to avoid over-estimating the level of disturbance at native parrot nests due to the recordings at this nest, the disturbance data from this nest were not included in the analysis.

The parrot nests were subject to significantly higher levels of disturbance than the common myna nests (Independent Samples Mann-Whitney $n_{\text{(myna)}}=6$ - $n_{\text{(parrots)}}=7$, $U=$

35.5, $P=0.035$). When we separated the disturbances into separate categories, only the rates of disturbance due to competitors differed significantly across native parrots and mynas (mean number of pictures per day: Independent Samples Mann-Whitney $n_{\text{(myna)}}=6$ - $n_{\text{(parrots)}}=7$, $U=39$, $P=0.008$; Fig 4). Comparisons involving the mean number of intruder pictures per day ($U=23.5$, $P=0.731$) and the mean number of predator pictures per day ($U=27$, $P=0.445$) revealed no significant differences between myna and parrot nests.

The mean number of conspecific pictures per day showed that common mynas were present significantly more frequently at their nests than native parrots (Independent Samples Mann-Whitney tests, $n_{\text{(mynas)}}=6$; $n_{\text{(parrots)}}=8$; $U=1$, $P=0.001^{**}$; Fig 5). Based on a small sample size of 13 nests, the relationship between nest attendance was in the direction expected (higher nest attendance, reduced nest disturbance), but was not significant (Pearson correlation: $R=-0.2$, $P=0.507$). In addition, we found no evidence that parental attendance and nest disturbance varied significantly as a function of nest outcome (success or failure); Independent Samples Mann-Whitney tests, parental attendance: $n_{\text{(failure)}}=4$; $n_{\text{(success)}}=9$; $U=26$, $P=0.217$; nest disturbance: $n_{\text{(failure)}}=4$; $n_{\text{(success)}}=9$. $U=26$, $P=0.260$.

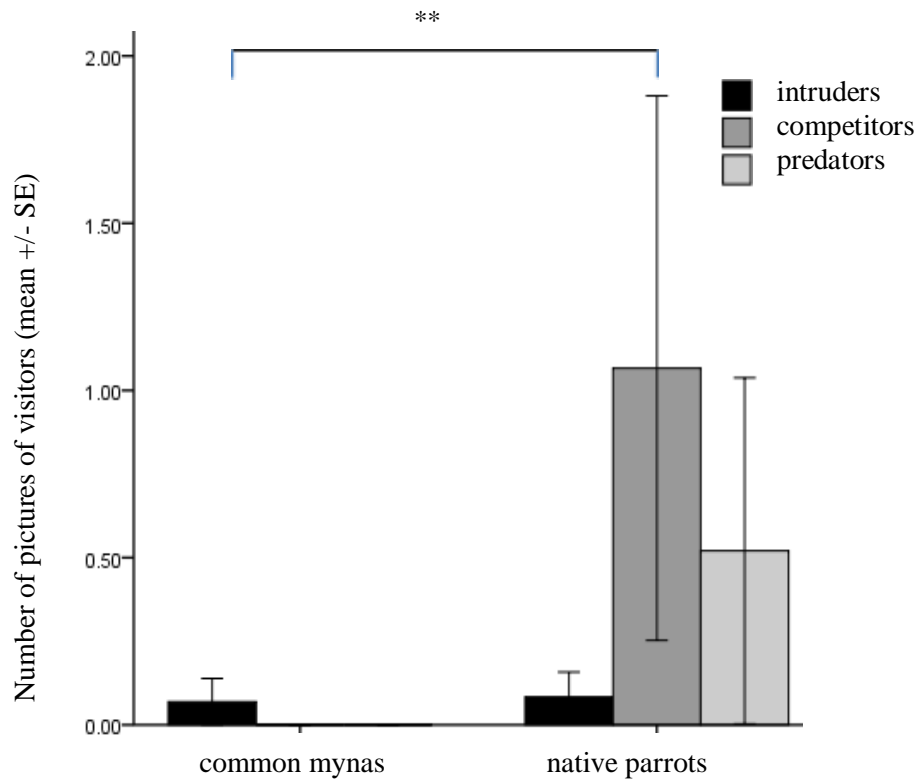


Figure 4. Daily disturbance by intruders, competitors and predators in common mynas and native parrots.

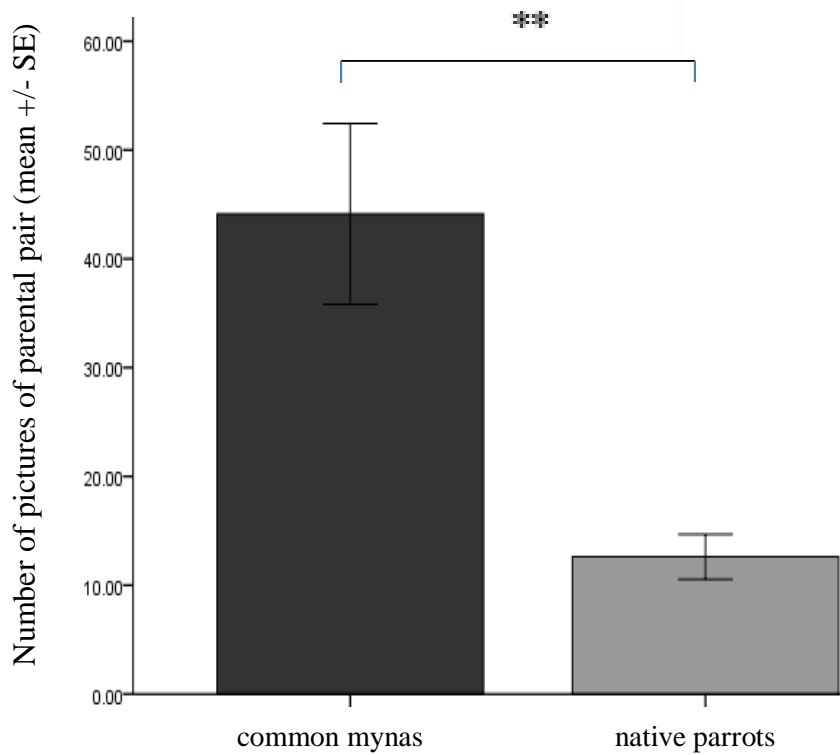


Figure 5. Daily visible parental nest attendance in native parrots and common mynas.

Discussion

In order to investigate whether the invasive common myna is a more successful breeder than native parrots in urban habitats, this study compared the nest box occupancies and breeding success of common mynas and native parrots in several urban locations in New South Wales, Australia. In parallel, using a subset of nests, we measured the levels of parental attendance and nest disturbance to investigate whether those factors could differ between native and invasive species and impact their reproductive success. Common mynas exhibited a higher level of reproductive success than native parrots (mostly eastern rosellas). Mynas were seen more often at their nest and mynas nests underwent lower level of disturbance compared to native parrots, principally from competitors. We found no evidence that breeding success differed between recently and long-established populations of mynas. Across both populations, common mynas produced significantly more fledglings than native parrots despite similar levels of nest box occupancy, in line with results by Garrock et al. (2013). In contrast with analyses in Canberra, however, no parrot nest failure was due to a common myna take over (Garrock et al. 2013). In the present study, we found no evidence of competitive interactions between mynas and native parrots around nesting resources.

Greater fledgling rates arose not because common mynas laid more eggs per clutch, nor because they produced more clutches, but rather because they successfully parented more chicks through to the fledging stage. In other words, mynas experienced significantly lower levels of nest failure than native parrots. Overall, 50% of parrot nests failed, the main cause of failure being hatch failure. Based on our existing knowledge, we can only speculate about why so many parrot eggs failed to hatch.

First, the nest box design used in the present study was selected based on previous research and intended to be attractive to both common mynas and native parrots (Pell and Tidemann 1997; Tidemann et al. 2011; Grarock et al. 2013). While very similar occupancy levels suggest that the boxes were equally attractive to both species (assuming that occupancy is not density-dependent), we cannot be certain that the box design was not more favourable to the breeding of mynas than parrots. For example, a recent study has revealed that nest box design and thermal insulation materials affect internal temperature and then could impact breeding success (Larson et al. 2018). As we did not measure nest box temperature, we cannot comment on how this variable might have affected breeding success of mynas and parrots. More work is certainly needed on identifying and measuring key nest box parameters that maximize breeding success for native birds.

Second, Australia is well known for its environmental uncertainty and lack of high quality territories (Low 1978; Webster et al. 2010). These environmental conditions are thought to underpin the very high prevalence of communal breeding in Australian birds (Ford et al. 1988; Cockburn 1996; Jetz and Rubenstein 2011; McDonald 2014). The present study was undertaken in urban environments where competition for natural nesting cavities is likely to be intense due to the increasing rarity of this resource (Harper et al. 2005; Davis et al. 2013). Under these conditions of high competition in both natural and anthropogenic environments, nest boxes might provide additional breeding opportunities for younger and less competitive eastern rosella pairs. First-time breeding eastern rosellas might lack the necessary experience to care appropriately for their eggs, which might in turn explain high levels of nest failure found in the present study. Clearly, longer term nest box monitoring is needed. Longer-term nest box monitoring across several breeding seasons, coupled with individual

marking of breeding native parrots, would help confirm or refute this hypothesis by determining whether individual breeding success increases with experience. Perhaps due to being first-time breeders or perhaps for some other reason, it is also possible that parrots in the present study produced high levels of infertile eggs. Future research should investigate eggs' fertility to determine whether this is the case.

Third, it is possible that under certain circumstances, differences in parenting style might be an important factor contributing to the breeding success of common mynas. Common mynas displayed significantly higher levels of parental nest attendance than native parrots and significantly lower levels of nest disturbance. A meta-analysis of North American and European invasive bird species has suggested that nesting habits and level of parental care are negligible influences on invasiveness (Jeschke and Strayer 2006; Jeschke and Strayer 2008). However, this question of parental care was limited to comparing mono-parental and bi-parental species to predict introduction success in New-Zealand (Sorci et al. 1998) or other oceanic islands (Mclain et al. 1999). More recent discussion papers on factors favouring invasiveness (Sol et al. 2002) or on factors involved in each step of the invasive process (Chapple et al. 2012) have underlined that a higher level of parental care seems to promote invasive success. In this study, we extended the question of level of parental care to native and alien bird species which presented the same type of parental care. That is, all were secondary cavity-nesting species with both parents committed to caring for the nestlings. To our knowledge, this represents the first comparison of a native and an alien species with similar bi-parental care systems. Our findings, in line with previous work, support the general idea that high levels of parental care assists alien bird breeding success.

We found that mynas visited their nests much more frequently than eastern rosellas. Furthermore, myna nests experienced significantly lower levels of disturbance

than rosellas, especially from competitors. These findings point to a potential causal relationship between increased nest attendance and reduced nest disturbance. Some studies have already demonstrated that under high food conditions, parents spend more time at their nest exhibiting antipredator behaviours, increase their chick provisioning rate and, consequently, decrease nestling begging that make nests less localizable by predators (Lendrem 1979; Smith and Montgomerie 1991; Rastogi et al. 2006). Although, the present study found no evidence within species that nests where parents were more present experienced fewer disturbances, it is likely that this relationship only becomes influential (and therefore detectable) in nests that, for some reason, are subject to high disturbance levels because it is only under those circumstances that nest attendance becomes beneficial. For example, when a pair experiences a potential nest take-over by another secondary cavity-nester, a high level of nest attendance might prevent nest intrusions and could lead to a favourable outcome while a low level of parental attendance might lead to clutch abandonment. An alternative explanation for why common mynas underwent less nest disturbance than native parrots is that their non native status allows them to escape from native intruding species. For example, the enemy release hypothesis is one of the major hypotheses explaining invasion success (Colautti et al. 2004; Liu and Stiling 2006; Shwartz et al. 2009). This theory promotes the idea that invasive species are successful in their invading range because they have left behind their co-evolved enemies in their native range (Maron and Vilà 2001; Keane and Crawley 2002). However, in our study level of disturbance by predators was the same in native and invasive species. Our cameras were placed only in long established populations and future research should investigate nest disturbance in long-established and recently-established common myna populations to test whether myna pairs experience more disturbance as a function of time since arrival.

It is possible that the differential level of nest attendance in common mynas and eastern rosellas is not the evolutionary end product of nest competition, but is merely attributable to differences in the diets of common myna and eastern rosella chicks (Moeed 1975; Cannon 1981). Common myna chicks are fed exclusively on insects and small invertebrates for the first ten days of their lives and then on other items (e.g. bread products and pieces from road trash or garbage) (Counsilman 1971). Parents carry each item in their mouth directly from the foraging site to the nest and then can only feed one chick per visit. In contrast, a parent rosella can forage and eat different items before joining the clutch and regurgitate to several chicks during each visit (Krebs et al. 1999; Krebs and Magrath 2000; Spoon 2008). This pattern of chick feeding would require fewer visits to the nest per unit of time. In addition, rosella chicks need to be fed a diversity of food items to develop (not just arthropods); this might require parents to forage on larger areas than mynas and stay away from the nest for longer periods of times. Differential feeding patterns would hence lead to differential levels of nest attendance and indirectly provide the benefits of nest guarding in environments where competition for nesting resources is high.

Our study shows that the higher breeding success of common mynas relative to native parrots might be a consequence of a greater visual and auditory presence at the nest by common mynas, rather than overt aggression, which might in turn reduce the levels disturbance in high competition environments and improve fledgling success. However, other factors than differences parental style could be involved in lower breeding success of parrots. It would be interesting for future studies to compare parrot breeding success in cities with and without mynas in order to measure the impact of mynas on parrot breeding. Future research should also aim to examine native parrots breeding success across several successive seasons to quantify the relative role of

breeding inexperience in shaping the lower breeding success of native parrots. Furthermore, the role of parental care could be investigated simultaneously with other contributing factors, such as levels of parasitism and/or levels of urban noise.

Overall, the results of this study point to the possibility that level of parental care may provide invasive birds with a breeding advantage relative to native birds when breeding in urban areas. Hence, invasion science can benefit from a broader view of the factors that contribute to making invasive species are so successful and of the ways they compete directly (e.g. via overt aggression) but also indirectly (via their inherent behavioural characteristics) with natives. While substantial research has focused on the former, almost no consideration has been given to the latter.

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Chapter 4:

Do native birds drive away invasive birds from urbanised Australia?

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Abstract

The noisy miner is a highly aggressive native Australian bird species whose density is negatively associated with avian abundance and richness. The noisy miners are endemic to eastern and south-eastern Australia in both rural and urban habitats. Miners have been shown to be highly aggressive both within the species and towards other bird species. They seem to be particularly aggressive in urban areas where introduced birds such as the common myna, occur. The common (Indian) myna (*Acridotheres tristis*) was introduced to Australia in the 19th century from Asia and is expanding its range in NSW and QLD. Here, we aimed to determine how behavioural interactions between the native noisy miner and the introduced common myna impact the invasive common myna's range expansion. We experimentally studied noisy miner responses to territorial intrusions by the common myna and compared them with the responses of noisy miners to conspecific and novel bird species intrusions in both urban and rural environments. We also compared noisy miner response to intrusions in areas with both long established (>40 years) and recently-established (<10 years) common myna populations in order to investigate whether the response could vary as a function of the period of

time both species overlap. We discovered that urban noisy miners displayed higher levels of aggression towards the common myna compared to a conspecific and the level of aggressiveness was the same in both long-established and more recently established myna locations. In an experimental setting using bird mounts and playbacks, noisy miners did not respond to a novel bird, nor to common mynas and conspecific mounts in rural habitats. By displaying a high level of aggression towards the species with which they already coexist in urban areas and presumably, based on their lack of response to a novel bird, ignoring them when they first encounter them, the noisy miners might contribute to the spread of the myna common in new areas.

Key words: invasive species, noisy miner, common myna, aggressiveness

Introduction

Ever since Konrad Lorenz wrote his book chapter entitled ‘What Aggression is Good For’ (Lorenz 1966), ethologists and behavioural ecologists have been exploring the role of inter- and intra-specific aggressions on animal assemblages. Because intraspecific aggression plays a key role in the structure of populations, this topic has received substantial interest over the years (e.g., Magurra and Seghers 1991; Cubaynes et al. 2014), especially as aggressive behaviour is involved in mate choice and thus in sexual selection (West-Eberhard 1983; Rosvall 2011). The research attention given to interspecific aggression is also preeminent. Aggressive interactions between species are important components in structuring animal communities (Caro and Stoner 2003; Grether et al. 2009; Howes et al. 2014; Grether et al. 2017). This is particularly true when species are competing for limited resources (Robinson and Terborgh 1995; Mac Nally and Timewell 2005; Weinstein and Graham 2016).

The case of high aggressiveness in a range of Australian birds is unique and especially interesting (Low 2016). Indeed, Australian birds display a high level of aggressiveness, which was hypothesized by Low (2016) to be related to the seasonal nature of nectar production in Australian trees. Australian trees (mostly of the genus *Eucalyptus*) grow with limited access to nutrients due to the poverty of the soils in many parts of the island continent (Milberg and Lamont 1997; Orians and Milewski 2007). The result of this particular situation is an excessive production of carbonates via photosynthesis, which cannot be involved in tissue production but which is allocated in nectar exudation (Orians and Milewski 2007). Secreting nectar is a method used by plants to encourage pollination by providing a highly sugary fluid. Profusion of nectar requires pollinators to disperse it and Australia abounds in vertebrate pollinators (Ford et al. 1979; Orians & Milewski 2007). The largest Australian bird family is the Meliphagidae family (honeyeaters) with 69 species (Keast 1968).

Australian honeyeaters are numerous and vary in size, weighing from 8 to 180 g (mean = 37g), yet are on average larger than convergent honeyeaters in other parts of the world, which are represented by the hummingbirds that weigh from 2 to 20 g (mean = 5g) (Orians and Milewski 2007). Honeyeaters and some other Australian bird species such as silvereyes (*Zosterops lateralis*) and rainbow lorikeets (*Trichoglossus moluccanus*) often interact around flowering plants because nectar is not like other food items (Ford et al. 1979). Plants supply nectar all day long and regularly renew their production over several days. Consequently, nectar is a renewable, but also temporally and spatially predictable resource, and it therefore pays off to defend, potentially leading to the evolution of aggressive defence of foraging territories (Beehler 1994; Ford & Paton 1976; Ford & Paton 1982; Low 2016).

Another environmental factor that can affect aggressiveness within the animal kingdom is increasing urbanisation (Miranda et al. 2013). Increase in aggressiveness in urban populations compared to rural populations has been demonstrated, for example, in gray squirrels (*Sciurus carolinensis*) (Parker and Nilon 2008), in Eurasian coots (*Fulica atra*) (Minias 2015), in blackbirds (*Turdus merula*) (Gliwicz et al. 1994) and also in song sparrows (*Melospiza melodia*) (Evans et al. 2010). This change in aggressive behaviour when individuals occur in urbanised areas, often coupled with a high tolerance to human disturbance, is sometimes termed the urban wildlife syndrome (Warren et al. 2006; Parker and Nilon 2012; Lowry et al. 2013). The main explanation for this behavioural change is that species in natural vs. urban areas often differ in their population abundances. Many cities hold much higher avian population densities than rural ones, sometimes up to 30 or 100 times superior (Moller et al. 2012) due to smaller number of species found in large densities in urban areas (Chace and Walsh 2006; Sol et al. 2017). This difference in population densities between urban and rural habitats is likely to result in different agonistic occurrences in both habitats (Shochat et al. 2006; Anderies et al. 2007). Some authors (Shochat et al. 2006; Anderies et al. 2007) proposed that natural areas under low bird densities can promote competition for mates, but this competition is essentially intraspecific and limited in time at the breeding season, whereas urban environments under high bird densities might stimulate intra and interspecific competition for anthropogenic food all year long.

The noisy miner (*Manorina melanocephala*), an Australian honeyeater, is an excellent model for studying interspecific aggression and its impact on avian diversity across a gradient of urbanisation (Lowry et al. 2013). A field study has shown that noisy miners can exhibit between two and three attacks per hour towards other birds within their colonies without discrimination (Scott D Piper and Catterall 2003) and their

agonistic dominance perturbs and induces changes in avian structure and diversity (Robertson and Gaines 1986; Robinson and Terborgh 1995; Mac Nally and Timewell 2005). This despotic bird has been shown to aggressively lead to exclusion of other species from its territories, especially of smaller avian competitors (Dow 1977; Grey et al. 1997; Parsons et al. 2006), leading to the decline of numerous small avian species in multiple study areas (Grey et al. 1997; Scott D Piper and Catterall 2003; Maron and Kennedy 2007).

The natural habitat of the noisy miner is often depicted as open or sparse parcels of grass in small woodland remnants (Dow 1977; Oldland et al. 2009). However, with habitat loss and fragmentation over the last decades, noisy miners have become abundant in urban parks, suburban and urban areas, presenting a potential new threat to the species already present (Catterall 2004; Sol et al. 2012; Haythorpe et al. 2013). This recent range expansion into suburban and urban habitats have led to an investigation of their aggressive responses towards disturbance as a function of the level of urbanisation (Lowry et al. 2011; Rudder 2016). Urban noisy miners, after being alerted by alarm calls, respond more aggressively to the broadcast of an aversive acoustic stimulus (a startling sound) than their rural counterparts (Lowry et al. 2011). Urban noisy miners also display higher levels of aggression than their rural conspecifics when listening to a playback of conspecific alarm calls followed by a playback of calls from Silvereyes (Rudder 2016).

Since noisy miners have negative effect on avian assemblages, we aimed to test the hypothesis that noisy miners have substantial impacts not only on native species, but also on invasive alien species populations, which in this way may practically act as “barriers” for invasive proliferation. In Australia, the main invasive urban exploiter is the common (Indian) myna (*Acridotheres tristis*).

The common myna is an urban exploiter (Shwartz et al. 2009; Orchan et al. 2012; Sol et al. 2012, Kark et al. 2013) and is much more abundant in urban habitats than in rural areas in its Australian range (Sol et al. 2012; Old et al. 2014). The noisy miner is considered as an urban adapter and is abundant in both rural and urban habitats (Lowry et al. 2013). Both species are heavily associated with anthropogenic food, display similar shape and weight (Fig.1), making them potential direct competitors (Haythorpe et al. 2013). Thus, we hypothesize that the native species would make the establishment of common mynas more difficult in invading new areas.

In this study, we aimed to investigate noisy miner aggressiveness towards territorial intrusions by different bird species as a function of habitat (rural vs urban). We also explored noisy miner territorial defence as a function of time they were overlapping with the invasive common myna. We addressed the following questions: (1) Are noisy miners more aggressive towards invasive common mynas compared with other bird species? (2) Does aggression vary as a function of how long the two species' ranges are sympatric? (3) Are noisy miners more aggressive towards heterospecifics and conspecifics in urban areas where the invader is present compared with rural habitats? To explore all these questions, we experimentally simulated territorial intrusions using a range of taxidermy and artificial mount species in rural and urban noisy miner colonies along the common myna invading range in New South Wales (in long- and recently-established populations of common mynas).

We predicted that noisy miners: (1) would be more aggressive towards common mynas than towards conspecifics or novel birds; (2) would exhibit higher levels of aggression towards common mynas when they had only recent historical experience with them; (3) would be more aggressive in urban than in rural habitats because this species seems to follow the urban wildlife syndrome.



Figure 1. Bird species used in the study. Left: noisy miners; right: common mynas. (Photos by Françoise Lermite)

Methods

Study locations

In add months 2016- 2017, we studied 35 study sites with 35 different noisy miner colonies in NSW, Australia (Fig 2). Study sites were chosen in rural and urban areas along the common myna's non-native range (Table 1). We used the Atlas of living Australia (website at <http://www.ala.org.au>) to identify locations where common mynas have recently (recent decade) established breeding populations and locations where mynas have been well established for at least forty years.

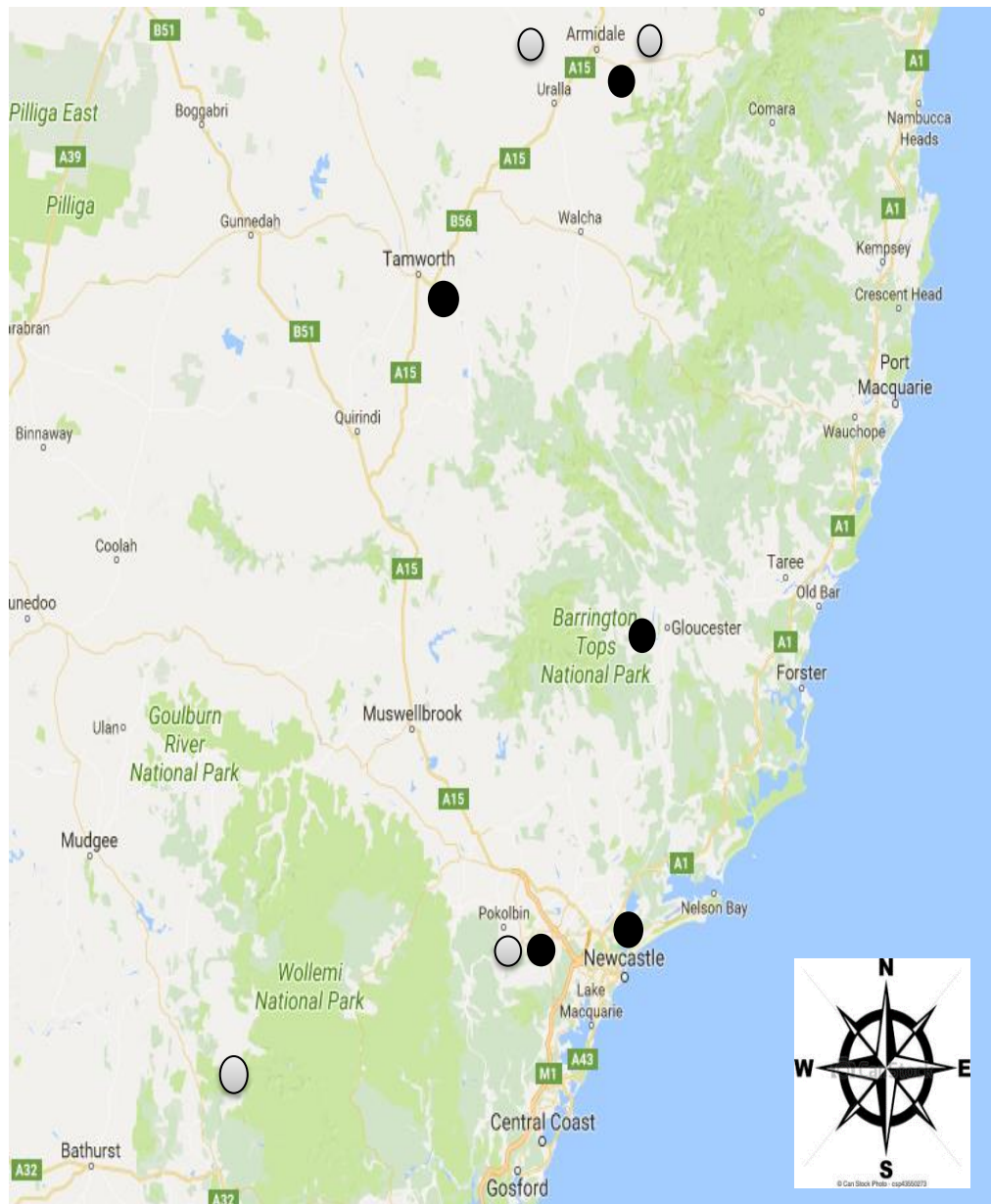


Figure 2. Study site locations in NSW, Australia. Black dots represent urban sites and grey dots rural sites.

Table 1. Study sites along the common myna non-native range in NSW, Australia. Old refers to long established populations of common mynas (at least 40 years), recent refers to areas where there is only evidence that common mynas started breeding during the recent decade and absent refers to remote rural areas where mynas are absent.

Locations of noisy miner colonies	Number of sites	Habitat		Populations of common mynas		
		Rural	Urban	Old	Recent	Absent
Armidale University	1		x		x	
Armidale High School	1		x		x	
Dumaresq Dam	1	x			x	
Hillgrove (Armidale area)	3	x				x
Newholme (Armidale area)	2	x				x
Tamworth	1		x		x	
Gloucester cemetery	1		x		x	
Newcastle University	3		x	x		
New Lambton	3		x	x		
Waratah	1		x	x		
Newcastle centre	3		x	x		
Jesmond	1		x	x		
Birmingham gardens	2		x	x		
Lambton	3		x	x		
Cessnock area	2	x		x		
Cessnock	1		x	x		
Carpertee Valley	6	x				x

North
Direction of the common myna invasion wave
South

Mount presentations

In order to compare aggression levels of noisy miners from urban and rural habitats, we presented a conspecific mount on each of the 35 territories (Fig 3, Table 1). To compare the levels of aggression displayed by noisy miners as a function of the time they have been exposed to the invasive common myna, we also presented a common myna mount on each of the noisy miners' territories in old and recent populations of common mynas. To quantify noisy miner response to an avian species they were naive to, we undertook a presentation of a mount that bore no resemblance to any avian species noisy miners would have encountered in the wild on a subset of territories (18 of the study sites). The mounts were presented at intervals of at least 24 hours in a random order on each territory and two mounts of each species was used within sites to avoid pseudo replication. The novel mounts consisted of two artificial birds, one blue and one red, one of each was selected randomly to be used on each territory (Fig 3c).

Presentation of each mount was accompanied by a 2.5 min playback of vocalizations belonging to the species of focal mount at the level of 80 dB in order to attract the attention of the birds on the site towards the mount and its identity, followed by 2.5 min of silence. In order to measure the response to a territorial intrusion rather than to danger, contrary to previous studies which employed noisy alarm calls to trigger attention (Clarke and Oldland 2007; Lowry et al. 2011), we chose to broadcast songs rather than alarm calls. Noisy miner songs were recorded in two different locations 150 km apart and these locations were not used as study sites to ensure broadcast calls were not familiar (i.e. such as those from neighbouring territories) to the tested noisy miners. The same procedure was applied to the recordings of common myna songs. A playback song of great tits (*Parus major*) (www.xeno-canto.org) was played during the novel bird presentations.



Figure 3. Specimens used for mount presentations. (a) common myna, (b) noisy miner (c) blue and red novel birds

For each presentation, the mount and a speaker were set up under a dark cloth in a relatively open area in noisy miner territories to ensure that the intruder could be detected easily. When at least two noisy miners were visually or acoustically detected within a 30 m radius from the experimental device, the cloth was removed and a video camera, focused on the direct vicinity of the mount, started to record the experiment. The camera was set up on a tripod approximately 25 m away from the experimental setup. All noisy miner behaviours were recorded using the video camera for five minutes in total, which included the 2.5 min playback and a further 2.5 mins post-playback period.

Noisy miners mostly demonstrated aggressive behaviour in groups of at least two individuals and aggressive responses were rarely expressed by only one individual. We encoded the aggression level of the response by scoring noisy miner behaviour using the common method of establishing a scale from 1 to 5 (McLean et al. 1986; Duckworth 2006; Carrillo and González-Dávila 2013). A score of 1 indicated that no aggressive response was detected and a score of 4 and 5 indicated the higher levels of aggression (see Table 2). These two last scores were used when at least one noisy miner pecked the mount. We chose the threshold of six contacts to attribute the highest score

of 5 to reflect the situation where some mounts were attacked for the entire duration of the presentation with a large number of pecks as compared to briefer attacks with only very few pecks. Since several birds responded to the stimulus, we decided to attribute a score to the colony tested using the higher score displayed by at least one individual of the group of miners. For example, if three birds interacted differently with the mount, one approaching, another one swooping and the third one pecking four times the mount, we established the score of four for this noisy miner colony. We also recorded the latency to attack the amount. In cases where noisy miners did not respond to the mount, the latency to attack was capped at 301s (i.e. latency = entire duration of the trail).

All procedures were approved by the animal ethics committee of the University of Newcastle (ARA A-2014-424).

Table 2. Criteria for scoring aggressive behaviour of noisy miners

Score	Behaviour description	Number of attacks
1	No response was detected	0
2	Exploratory approach to 20 cm of the mount	0
3	Flights and swoops toward the mount	A least one
4	Physical contacts: pecks	< 6
5	Physical contacts: pecks	> 6

Data Analysis

In order to examine the factors that influenced levels of noisy miner aggressiveness towards a territorial intruder, we fitted a generalised linear mixed model (GLMM) with a Poisson distribution and a log link to the distribution of aggressiveness scores (Lme4 R package, Bates et al. 2014). Because rural noisy miners never displayed any aggressive response towards any of the mounts, and because neither urban, nor rural noisy miners responded aggressively towards the novel bird mounts, we fitted this GLMM model to the distribution of aggressive scores excluding data collected in rural

habitats and during presentations of the novel bird. We included Mount identity (conspecific/common myna), as well as season (breeding/non-breeding) and invasion stage (recent/old populations of common mynas) as predictor variables. Study sites were included as a random factor.

In order to study the differences in the latency of noisy miners to respond to conspecific and common myna territorial intrusions, we fitted a Cox Proportional Hazards model to the latency to attack values (coxme R package, Therneau 2015). Latencies to attack the mount included capped time values for cases when no attack occurred. Therefore, we used this nonparametric survival framework which requires few assumptions and allows the inclusion of covariates and random factors while treating capped latencies (more typically death, but in this case latency to attack the mount) as censored observations (Crawley 2002). Mount identity (common myna/conspecific), invasion stage (recent/old populations of common mynas) as well as season (breeding/non-breeding) were included as predictor variables. Study site was entered as a random factor. All statistical analyses were carried out using R version 3.2.2 (R Core Team 2015). Two-tailed tests were used throughout and alpha levels were fixed at 0.05.

Results

Urban noisy miners displayed a significant higher response towards common mynas (mean aggressive score = 2.67 ± 0.33 SE) than towards their conspecifics (mean aggressive score = 1.76 ± 0.26 SE); (Poisson GLMM, $Z = -1.956$, $P = 0.05$) (Table 3, Fig 4). The levels of noisy miner aggression were similar over the breeding and the non-breeding season and in long-established and recent populations of common mynas (Table 3).

Table 3. Predictors of noisy miner aggressiveness. Results of GLMM on aggressive score. Bolded p-values were below a 0.05 threshold of significance.

Parameter	Estimate	Std Error	Z value	<i>P</i>
Trial (noisy)	-0.414	0.211	-1.956	0.050
Population (recent)	-0.055	0.268	-206	0.836
Season (breeding)	0.160	0.207	0.775	0.438

Reference categories of variables are noted between brackets near the variable name

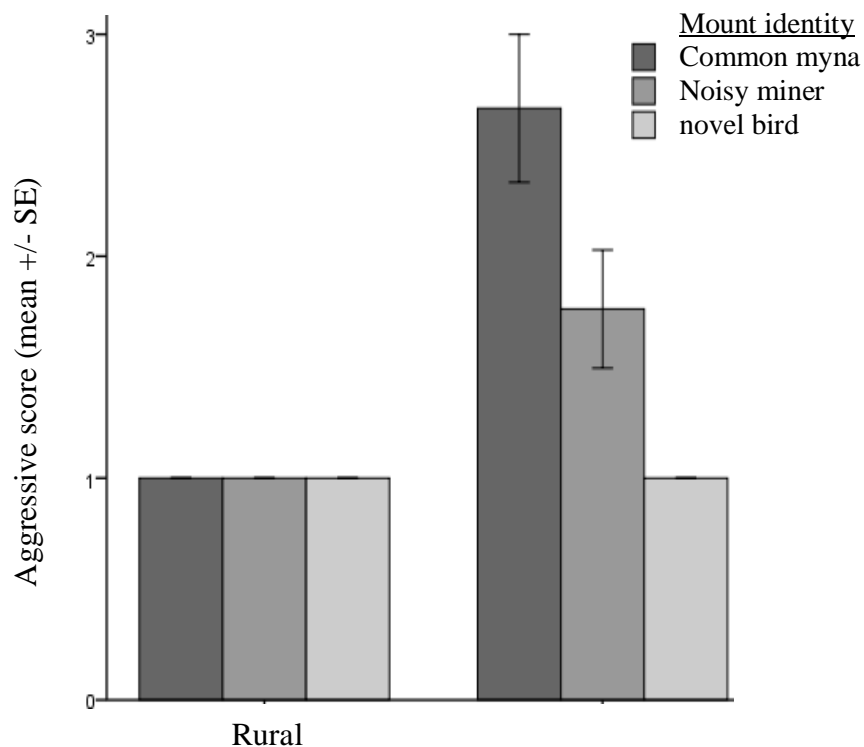


Figure 4. Noisy miner response towards conspecific and heterospecific bird intrusions in urban and rural territories.

We found that urban noisy miners attacked common myna intruders significantly faster than noisy miner intruders (Cox Proportional Hazards model $Z=-2.27$, $P=0.023$) (Table 4, Fig 5). Noisy miner attack latency did not differ as a function of the duration of sympatry of their range with breeding mynas (Fig 5), nor between the breeding and the non-breeding season (Table 3).

Table 4. Cox Proportional Hazards model on the latency to attack common mynas and conspecifics intruders in urban habitats.

Parameter	Coefficient	Exp (coefficient)	SE (coef)	Z value	<i>P</i>
Trial (noisy)	1.098	0.333	0.483	-2.27	0.023
Population (recent)	0.391	1.478	0.574	0.68	0.500
Season (breeding)	0.301	1.352	0.495	0.61	0.540

Reference categories of variables are noted between brackets near the variable name

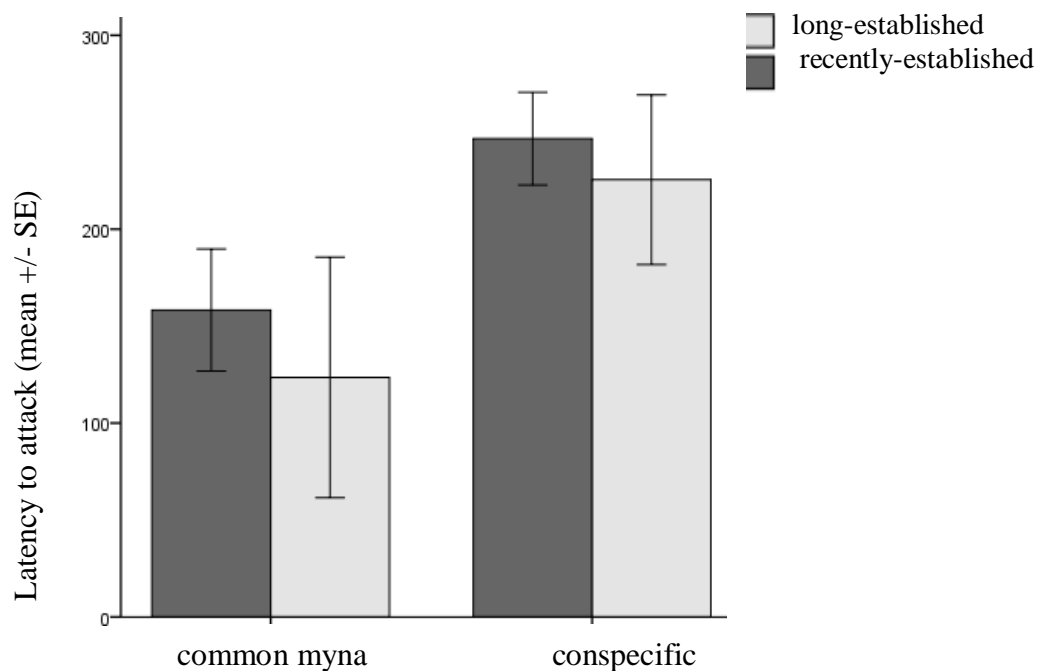


Figure 5. Noisy miners means latency to respond to common mynas and conspecific intrusions +/- SE across common myna invasion range (long and recent-established populations of common mynas).

Habitat was the best predictor of noisy miners' responses towards all types of intrusions. Noisy miners belonging to rural colonies never showed any aggressive response towards any of the intruding species while their urban counterparts expressed different levels of aggressive responses (chi-square = 16.296, df=4, p=0.003; Fig 3). In both populations, the novel birds were left undisturbed by the noisy miners (chi-square = 6.655, df=4, p=0.032; Fig 3).

Discussion

The noisy miner's ability to exclude many other bird species from their territories (Dow 1977; Grey et al. 1997; Parsons et al. 2006) and its propensity to increase aggressiveness in urban territories (Lowry et al. 2011; Rudder 2016) lead us to ask whether noisy miner aggression and intense territorial defense could act as a barrier to urban invasive species, such as common mynas. In line with our predictions, urban noisy miners displayed more aggressive behaviour than did rural ones and they exhibited a quicker and higher aggressive response towards common mynas than towards conspecific intruders. However, invasion stage (old or recently established populations of common mynas) did not play a role in noisy miners' interspecific aggressiveness.

As predicted, urban noisy miners responded aggressively towards intrusions. However, surprisingly, rural birds, rather than showing a lower level of aggression, entirely ignored the three types of intruders, namely a conspecific, a common myna and a novel bird. We explored noisy miner aggressiveness towards intruders a step further than the only two studies that have explored the noisy miner aggressiveness in urban and rural habitats (Lowry et al. 2011; Rudder 2016). Contrary to the two studies who found that birds in rural populations were less aggressive than the urban ones but at

least exhibited some level of response, we did not record any response. Furthermore, all studies demonstrating the detrimental impact of noisy miner aggressions on bird communities occurred in rural areas, which implies that rural noisy miners can exhibit aggression under some circumstances (Grey et al. 1997; Scott D Piper and Catterall 2003). Two different reasons could explain our unanticipated finding (no response in rural sites). First, contrary to studies by Lowry et al (2011) and Rudder (2016), we used a song matched to the identity of the intruding species to attract noisy miner attention prior to presentation of the intruder, and not noisy miner alarm calls. Noisy miners are known to respond very reliably to conspecific alarm calls (Clarke and Oldland 2007; Kennedy et al. 2009) and this tendency is often used to estimate noisy miner density on a territory. When responding to conspecific alarm calls played back immediately prior to presentation of the stimulus of interest, noisy miners are responding to a signal for hazard before they have had the opportunity to identify the threat itself. Therefore, it is highly likely that the stimulus of interest is assimilated to a threat and individuals are primed to respond to it defensively when it subsequently appears in the same location. Moreover, alarm calls are associated with cooperative mobbing behaviour which is involved in competitive social behaviour (Kennedy et al. 2009). When aggressive and mobbing behaviours are activated by alarm calls it is probably difficult to disentangle the relative roles of social contagion and threat identification in activating the defence response. In this study, by avoiding the use of alarm calls as an attention-grabbing methodology, we suggest that we measured more accurately the extent to which noisy miners evaluated a stimulus to represent a territorial intrusion and the need to express aggressive territorial defence. Second, we did not only measure responses to noisy miner competitors. Despite these methodology differences, different levels of aggressiveness in urban and rural populations could also be due to different levels of

bird densities. Urbanized environments are well known to present a decline in species richness but also an increase in bird densities (Moller et al. 2012). Under these conditions, noisy miners must cope with higher densities of conspecifics and also higher densities of other urban adapters and exploiters such as the common myna. Noisy miners might respond to this situation by exacerbating their aggressive behaviour.

Studies quantifying the role of noisy miners in avian diversity decline have focused on shifts in diversity of other honeyeaters or in species feeding on alternative noisy miner food resources (Grey et al. 1997; Scott D. Piper and Catterall 2003). Yet it is known that noisy miners can tolerate other species that are not direct competitors, such as grey butcherbirds (*Cracticus torquatus*) (Grey et al. 1998; Loyn 2002). Here, we presented miners with avian species that do not compete with miners for nectar (mynas; unfamiliar birds) and did not prime noisy miners to respond aggressively via the use of alarm calls. Differential patterns of response across intrusions by common mynas and unfamiliar birds suggest that noisy miners' responses are sensitive to the degree of competition. Novel bird species coupled with an unfamiliar song did not generate any aggressive response in urban miners, and did not trigger any alarm or distress calls despite miners showing a clear inspection response. A lack of response is consistent the miners not perceiving unfamiliar birds as a threat. Without comparing responses to a large array of stimuli that vary along different dimensions (e.g. live vs. mounted; real vs. artificial feathers), it is not possible to know exactly how miners perceived the novel bird and therefore to completely exclude that the stimulus was not in some way impoverished (e.g. depicted the shape of a bird, but not real feathers). It is worth noting, however, that by comparison other static mounts paired with a song playback elicited a response, so lack of aggressive response to the novel bird mounts is unlikely to be attributable to lack of movement per se. However, the noisy miner's

response to novel birds indicates that they were not perceived as a threat. This finding points to a key role of experience in noisy miner hyper-aggressiveness: it appears that noisy miners might have to learn which intruders are a menace (predation or competition) either through direct or social learning (Griffin 2004; Platzen and Magrath 2005; Haff and Magrath 2013). On the other hand, common mynas might be perceived as an important competitor because they triggered a high defence response from the noisy miners. While these species do not compete over nesting sites (noisy miners build a nest whereas common mynas are secondary-cavity nesters) they probably do compete over food. While noisy miners belong to the *Meliphagidae* family and therefore feed on nectar (but not exclusively), their diet does overlap with that of common mynas (*Sturnidae* family), in that they both eat insects and anthropogenic food. It is not surprising then that noisy miners consider common mynas as competitors in urban areas. Following the same pattern than nectar-bearing trees are in wildlands, the anthropogenic food in urbanized zones is a temporally and spatially predictable resource, which is therefore worthwhile defending and favours active aggressive defense (Shochat et al. 2004; Shochat and State 2004).

The high level of aggressiveness of noisy miners towards common mynas was evidence in locations where breeding common mynas have been established for more than 40 years, and in locations where mynas have been breeding for less than a decade. Given that noisy miners do not respond to birds with which they have no experience (see response to novel bird), it seems that only a few years is long enough for competitive interactions to become established between a native urban adaptor like the noisy miner and an introduced urban exploiter like the common myna. Rapid emergence of aggressive behaviour is in line with the conclusion above that the identity of species against which territories must be defended is learnt. However, this learning process may

depend upon the outcome of the interactions between these two species (noisy miner and common myna). Two studies have quantified naturally occurring aggressive interactions between mynas and miners observationally, and all concluded that the invasive species was more often the recipient of the attacks and the native noisy miner was the winner of the conflicts (Haythorpe et al. 2012; Haythorpe et al. 2013; Lowe et al. 2011).

In the light of these two key findings, namely that noisy miners are highly aggressive in urban areas and that they only attack species with which they have prior experience, we speculate that noisy miner hyper-aggression might, instead of operating as a barrier to common myna range expansion, might in fact contribute to driving it. The patterns of noisy miners' responses towards intruders found here suggest that when common mynas invade novel areas, they are likely to be left undisturbed by noisy miners for a short window of time. Once they are settled and population density increases, the over-competition process operates, and noisy miners might contribute to driving common mynas further away. This assumption of successive different behaviours, noisy miners first tolerant then aggressive towards mynas, requires to be confirmed by testing some urban noisy miner colonies in the early phases of myna invasions.

There are still few areas of the coast of Queensland where noisy miner range does not overlap with that of common myna. An accurate investigation of the Atlas of Living Australia might provide some urban noisy miner colonies that are still myna-free. Then a careful monitoring of those areas should offer the opportunity to investigate in real time the reaction of those colonies when first invaded by common mynas.

This hypothesis also draws upon previously documented common myna responses to noisy miner hyper-aggressiveness. Recorded agonistic behaviours during

transects, and competition over experimental food patches, have shown that noisy miners were the most aggressive and won more conflicts than common mynas, the common myna being less aggressive than many native species, contrarily to the public's perception (Haythorpe et al. 2012; Lowe et al. 2011; Sol et al. 2012). These patterns suggest that in urban environments noisy miners are dominant over common mynas and therefore have the capacity to displace them and could promote their spread towards new places to colonize.

In summary in this study, we discovered that noisy miners exhibit an urban wildlife syndrome by increasing their level of aggressiveness as a function of the degree of urbanisation. We found that urban miners displayed high aggressiveness towards species with which they were familiar (i.e. sympatric), but not towards the mount of a bird species with which they were not familiar, suggesting that miner responses develop with experience of sympatry and perhaps also competition. Although one might argue that we cannot be certain what aspect of the novel bird made the miners decide not to attack it, we consider it unlikely that the novel mount was not recognised as a bird. Indeed, it had the characteristic shape of a bird, and was no different to the other mounts, in that they were also static but did elicit miner responses. In these conditions, noisy miners' hyper-aggressiveness towards the invasive common myna might not reduce myna populations. We propose another hypothesis: by ignoring individuals of an unfamiliar species when they first invade, and by troubling by repeated attacks the invaders later on, presumably once they reach densities sufficient that experience enables them to be recognised as competitors, the hyper-aggression of noisy miners might, rather than operating as a barrier, in fact facilitate the spread of this non-native avian species. Further research should investigate areas undergoing early stages of

common mynas invasion and compare both species densities in urban and rural environments.

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Chapter 5.

Common myna abundance and breeding behaviour as a function of habitat and invasion phase

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Abstract

The common myna (*Acridotheres tristis*) has been introduced in Australia over 150 years ago and is expanding its geographic range along Australia’s east coast and inland. The myna occurs mostly in urban areas. Little is known about how urban habitat selectivity might change as a function of invasion stage. Here, we examined the hypothesis that myna populations show changes in urban habitat selectivity as they expand their range from source to front populations. this study included two large-scale nest box experiments, that examined myna abundance and breeding behaviour as a function of habitat and invasion stage. In Part 1, we studied mynas at both ends (invasion front and source) of the southern Queensland (QLD) and New South Wales (NSW) invasion waves, whereas in Part 2, we focused on a sub-set of the study area, examining in more detail the NSW invasion wave, and included a more detailed comparison with native parrot breeding. We discovered that NSW mynas are significantly more common in urban habitats than in park and edge habitats, a difference that was not present in QLD, suggesting that NSW mynas may be more urbanized than

QLD mynas. Mynas were most abundant in urban habitats in front and source populations, but they were only more abundant in park habitat compared to the edge habitat in source populations, suggesting a pattern of expansion over time whereby mynas first occupy urban areas and then overflow over time into less urban environments as populations become established and grow. In both front and source populations, nest box occupancy was highest in the urbanised habitats, suggesting that competition over nesting resources might be highest in that habitat. Our detailed work in NSW showed similar levels of nest box occupancy by mynas and native parrots and a higher breeding success in common mynas. over three years of breeding both native and invasive displayed an equivalent reproduction rate. The contribution of these findings to a deeper understanding of the range expansion of the invasive common myna across Eastern Australia and implications for myna management are discussed.

Introduction

The spatial spread of invasive species has been the focus of significant theoretical and empirical research for many decades (Hastings et al. 2004). Originally modelled under multiple simplifying assumptions, including non-evolving species spreading through homogenous environments, invasive spread is now recognized to be a much more complex phenomenon than previously thought (Melbourne et al. 2007). A deeper understanding of spread and an improved ability to predict it, relies upon incorporating a rich array of biological information, such as spatial and temporal heterogeneity, species interactions, and evolution (Hastings et al. 2004).

In order to improve predictions of species invasion potential, invasion biology has focused heavily on identifying the ecological, demographic, and life-history factors associated with variation in invasion success across species (Cassey et al. 2004; Chiron

et al. 2009; Dyer et al. 2017; Hayes & Barry 2007; McKinney & Kark 2017; Sales et al. 2017). In birds, the most common approach has been to gather information on the success vs. failure of human-mediated introductions and to identify significant environmental predictors, often sampled by searching the literature (Blackburn et al. 2013; Sol et al. 2012). As a consequence, we know a lot about the predictors of variation in establishment success at the species level, but far less about the predictors of within-species variation in invasive spread.

One of the reasons for this knowledge gap is that a focus on spread rather than on establishment, and on within-species variation, rather than cross-species variation, requires a very different methodology. What is needed is a comparative analysis of a species' populations at different invasion stages (i.e. front of the invasion wave vs. back of the invasion wave), ideally replicated across different invasion waves. Changes in demographics indicative of a fast or slow-moving invasion front, and/or changes in life-history and species interactions, which might be associated with changes in range expansion rates, cannot be documented from an existing literature, but rather need to be measured on the ground. The information gained is critically important to improving the accuracy of spread estimates across different areas of an alien species' distribution. Although critical to managing many of the thousands of alien species that have successfully crossed the barrier of transport and establishment and are currently spreading, such research is comparatively high in cost and resources, and are therefore rare.

In 1862, ~100 common mynas were released for the first time in Australia in the city of Melbourne in order to control insect populations (McCoy 1885-1890; Gregory-Smith 1985). Further introductions occurred over the course of the subsequent decade (Long 1981). Mynas are reported to have been introduced to Sydney around the same

time (Hone 1976; Long 1981), and were later the source of human-mediated translocations to Canberra between 1968 and 1971 (Hone 1976). As Sydney birds form a separate genetic cluster to that of Melbourne, it is likely that source birds were also from overseas (Ewart et al. 2019). Melbourne mynas are reported to have been translocated to two cane fields in north QLD (on the Herbert and Johnstone rivers, between Cairns and Townsville) and in Townsville in 1883, to combat locusts and cane beetles (Chisholm 1919; Long 1981). Recent genetic analyses have revealed evidence for a third genetic cluster, located in southern Queensland. This cluster is the result of a translocation of either Melbourne or Cairns birds, and a ghost population, perhaps from overseas (Ewart et al. 2019).

While the abundance of mynas in the areas of initial introduction remained relatively low initially, expanding only slowly over many decades, since the 1940s however, the abundance and range of the species has increased dramatically (Hone 1976). As a result, each one of these historical introductions and human-mediated translocations has formed a new wave of ongoing range expansion. These replicated invasion waves provide a unique opportunity to quantify the demographics of birds at different stages of the invasion process, as well as to determine whether the interactions of alien birds and the physical and social environment change within and across invasion gradients.

Despite their significant population and range expansion in Australia over the past four decades, so far, most studies suggest that common mynas have remained relatively urbanized in Australia (refs). While being undoubtedly one of the most commonly observed species in city centers of the east coast, so far research has shown that their densities decrease along a gradient of decreasing urbanisation and increasing tree cover (Crisp & Lill 2006; Grarock et al. 2013; Long 1981; Parsons et al. 2006; Sol,

Bartomeus, et al. 2012). It is often assumed that this habitat-dependent distribution reflects an inherent preference of mynas for urban environments. Little is known about common myna habitat preference in their native range, however it seems that common mynas mostly occur around human (farm or cities). One study in central India (Moeed 1976) and another in West Bengal (Sengupta 1976) reported that common were abundant in both rural and urban habitat but always living around villages and nesting in buildings. Several authors have suggested that habitat restriction and preference for urban habitat minimizes the myna interactions with native species, and thereby lowers the impact of common mynas on native assemblages. Yet, other studies have noted that the myna is not a strong habitat specialist and has the capacity to occupy a range of environments both in Australia and elsewhere (Counsilman 1974; Crisp & Lill 2006). These patterns point to the potential for significant inter-individual variation in habitat preferences in mynas. Common mynas are a secondary cavity nesting species, and spread into less urbanized environments is bound to increase competition with native secondary cavity nesting species, particularly similar sized members of the parrot family (Tidemann et al. 2011).

To evaluate the potential for relative success of mynas in less urbanized environments requires some knowledge of the reproductive success of the species in those habitats. Contrary to the substantial amount of work documenting changes in myna abundance along an urban gradient (Haythorpe et al. 2013; Old et al. 2015; Sol et al. 2012), only one study so far has documented the reproductive behaviour of this secondary cavity nesting bird across different habitats. In a study monitoring over 200 experimental nest boxes in the Canberra region, Grarock and colleagues (2013) found that nest box occupancy was significantly correlated with myna abundance. Accordingly, decline in occupancy run parallel with decreasing abundances along a

gradient of increasing tree cover (Garrock et al. 2013). One possibility is that nest box occupancy is a direct consequence of myna abundance and, when mynas become more abundant, competition for nesting resources becomes stronger, pushing more birds to occupy boxes. In the same study, however, Garrock et al. (2013) found that, even though mynas were significantly less abundant and nest occupancy was significantly lower under medium than in low tree cover, egg success (% hatched) did not differ across the two habitats. Egg success only decreased significantly from medium to high tree density (Garrock et al. 2013). Assuming similar survival and emigration rates, this finding suggests that myna population growth has the potential to be as strong under medium levels of urbanisation as it is under high levels of urbanisation.

All work investigating myna abundances and reproductive success so far has been undertaken within long-established populations. As a result, it is currently not known whether mynas display variation in these traits along the invasion wave. Changes in habitat preferences could arise if dispersal away from source areas towards the invasion front is nonrandom relative to individual variation in the trait, generating spatial sorting along a gradient of trait variability, with the potential for directional selection via associative mating (Berthouly-Salazar et al. 2012; Phillips et al. 2006; Shine et al. 2011). Urban mynas are highly dependent upon anthropogenic foods (Sol et al. 2012), but also exhibit a significant preference for high-protein foods when offered a choice (Machovsky-Capuska et al. 2015; Peneaux et al. 2017). Some individual mynas might be prone to leaving habitats with high concrete cover, where they rely on anthropogenic foods (Sol et al. 2011), in search of habitats with more insects and higher-nutrient foods (New 2018; Pierotti & Annett 1987). A decreasing preference for urban habitats along the invasion wave has the potential to increase the impact of mynas on native avian assemblages by increasing their geographical overlap. Reduced

preferences for urban habitat, and a greater tendency to occupy non-urban ones, might also transform the common myna into a more significant agricultural pest in Australia than is currently the case, in particular to the grape industry. Determining whether habitat-specific distributions, and reproductive outputs change along the invasion gradient is therefore not only theoretically interesting, but also critically important to long-term management of this species and prioritizing management through space and time.

Here, we undertook a large-scale experimental nest-box study to compare mynas from long-established source geographic locations and mynas from recently-established invasion front areas. We studied mynas across three different habitats (urban, open park, edge) in each of our study sites. In the first part, we studied mynas for two successive breeding seasons at both ends (front and source) of the southern Queensland invasion wave, as well as the New South Wales invasion wave (front and source), quantifying myna abundance, nest box occupancy and breeding success as a function of invasion stage and habitat type. In the second part of the study, we undertook a geographically more detailed local (Hunter region, see below), but temporally longer (three vs. two years), analysis of myna breeding, and expanded our taxonomic scope to include a comparison with native parrot breeding.

Study 1

The aim of this study was to determine whether mynas show changes along an invasion wave in their tendency to occupy and breed in urban environments preferentially. To this end, we measured abundance, nest box occupancy and reproductive success in relation to both habitat (urban, open park, edge habitat) and invasion stage (front, source) in mynas at both ends (front and source) of the southern Queensland invasion

wave, as well as the New South Wales invasion wave (front and source), for two consecutive breeding seasons. Based on existing work, we predicted that mynas at the source would be more abundant, and nest box occupancy would decrease along a gradient from urban to park to edge habitat. Based on the simplest model of range expansion whereby mynas disperse from source populations, yet retain their preference for urban habitats, one would expect the same pattern to be present in front populations. Based on a more complex model of range expansion, whereby dispersal is nonrandom with respect to habitat preferences, we predicted that mynas would display a different pattern of abundance and nest box occupancy on the front relative to the back of the invasion wave.

Methods Study 1

Study sites

Eleven study sites, six in New South Wales (NSW) and five in Queensland (QLD) were selected using Australian historical atlas bird records from the past (Atlas of Living Australia, <http://www.ala.org.au>, see more details in McKinney and Kark 2017). NSW sites included two in long-established, ‘source’ geographical areas where mynas have been breeding for more than 40 years, and four recently established, ‘front’ areas where myna breeding has only been recorded in the last 10 years) (Fig. 1). In QLD, we applied the same criteria to select three source sites and two front sites (Fig. 1). Within each site, we installed twenty-four nest boxes, eight in urban habitat, eight in open parkland habitat and eight at the forest edge (Fig. 1 & 2; Appendix 1&3).

Nest box design

The internal dimensions of each nest box were 400 (H) x 170 (W) x 170 (D) mm and the entrance hole measured 65 mm diameter. This design was informed by former nest box studies to provide nesting opportunities for common mynas as well as other secondary cavity nesting bird species of approximately similar size (e.g. several native parrots) (Grarock et al. 2013; Orchan et al. 2012; Tidemann et al. 2011). Each box was fitted with a 75-cm external perch located approximately 3 cm under the entrance to allow birds to land on the box before entering. An internal ladder was carved out of the nest box internal wall to allow parents and chicks to access the box following Orchan et al (2012).

Bird surveys

Each month over a period of two years we conducted three point counts in each study site, one in each habitat in order to determine avian diversity and bird species abundances in each location (totalling 33 monthly point counts for eleven study sites across two years). We did all surveys in the mornings between 7 and 10 AM in summer and between 8 and 11 AM in winter following a uniform order. While standing approximately at the centre of each array of eight nest boxes (Fig. 1), we recorded every bird seen and heard within a 50 m radius for a period of 10 minutes. The counts were used to calculate a Shannon index (Spellerberg & Fedor 2003) and a common myna abundance for each site, each habitat, and each month.



Figure 1. Study sites on the east coast of Australia and example of nest box allocation to habitat. (a) Study site locations in NSW and Queensland. (b) Illustrative example (source site, New Lambton, NSW) of the nest box arrangement with eight boxes in urban habitat (green circles), eight in park (red triangles) and eight in the bush edge (yellow squares). For details see appendix 1&3.

Vegetation surveys

Circular surveys were conducted by only one investigator (AR), for consistency, to identify vegetation diversity and structure around each nest box to a 15-meter radius (Fig. 2). The percent ground cover of shrub, turf, and sealed ground (i.e. asphalt and concrete) was estimated from the centre of the plot (i.e. the tree to which the nest box

was attached). We also noted whether the tree to which the nest-box was attached was native or introduced.

We fitted a principal component analysis (PCA) to the percent vegetation values collected during the vegetation surveys (Table.1). The first axis explained 59.7% of the variance. The score generated by this first axis reflected the level of open land (eigenvector: 0.697) and the concrete cover (-0.714). Variable loadings indicated that lower scores referred to higher level of urbanisation. The second axis explained 40.2% of the variance and reflected the bush cover (0.908) with higher values referring to more bushy areas.

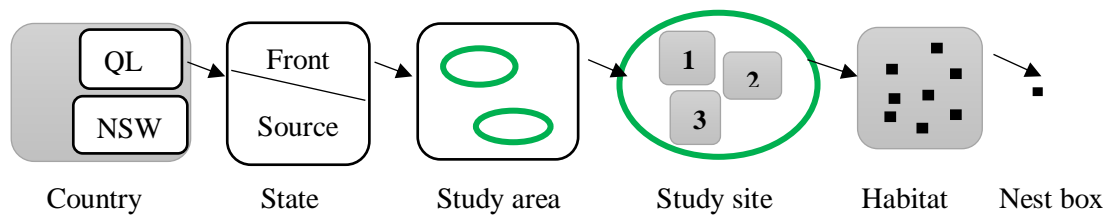


Figure 2. Diagram of scale hierarchy of the study from the national level to nest box unit. Bird surveys occurred at the habitat level and the vegetation survey at the nest box level.

Table 1. Orthogonally (Varimax) rotated component loadings on first and second axis for vegetation cover. Bold indicates those variables which contribute to a component meaning

	First axis	Second axis
Turf (open grass land)	0.697	-0.323
Sealed ground (asphalt and concrete)	-0.714	-0.262
Shrub and trees	0.041	0.908

Nest box monitoring

We monitored all nest boxes on a weekly basis using a gooseneck camera set up on a long plastic pole and connected to a Bluetooth monitor for nine months (Sept-May), a period that include the entire documented breeding season of common mynas on the East coast of Australia (October-April). During weekly monitoring, we collected information on the species occupying the nest box (species ownership), but also on number of attempts, eggs, nestlings and fledglings. We considered a breeding attempt had occurred each time a nest was found with at least one egg.

Mynas are reported to breed repeatedly in the same nesting site within the same breeding season (Counsilman 1971). Hence, it was reasonable to assume that the total number of attempts and fledglings recorded in each nest box for each year was produced by the same pair. We therefore calculated, for each box, the number of attempts per individual by dividing by two the total number of attempts recorded in a nest box during each breeding season. We repeated this calculation, for each box, using the total number of fledglings recorded in each nest box during each breeding season to obtain the number of fledglings per individual. We then used this variable as a measure of breeding success.

All procedures were approved by the animal ethics committee of the University of Newcastle (ARA A-2014-424) and by the University of Queensland (UQR&I Animal Ethics Unit AE23185).

Data analysis

Myna abundance

For each year of the study, we recorded the number of common mynas seen and heard at each study site and within each habitat. This variable was used as an outcome variable in a Poisson GLMM model with a log link function using the R package lme4

(Bates et al. 2014). We included state (NSW, QLD), invasion stage (front, source), year (1, 2), and habitat (urban, park, edge) as categorical predictors, as well as the interactions between state and habitat, invasion stage and habitat, and state and invasion stage. Species richness (Shannon index) was included as a continuous predictor variable. Study site was entered as a random factor. Significant interactions revealed by this model were followed up by Independent Samples Mann-Whitney tests and Wilcoxon Kruskal-Wallis tests for multiple comparisons.

Myna nest box occupancy

We calculated the number of nest boxes (max=8) occupied by common mynas in each site and habitat. This variable was used as an outcome variable in a zero-inflated negative Poisson mixed model with a log link function using the R package glmmTMB (Brooks et al. 2017). This model was selected to take into account simultaneously the high proportion of zeros (sites where no nest box was used by common mynas) and the over-dispersion of the data around zero (Zuur et al. 2009). We included state (NSW, QLD), invasion stage (front, source), year (1, 2), and habitat (urban, park, edge) as categorical predictors, as well as the interactions between state and habitat, invasion stage and habitat, and state and invasion stage. Species richness (Shannon index) was included as a continuous predictor variable. Study site was included as random factor.

Breeding attempts and breeding success in mynas

We fitted two Poisson GLMM models, each with a log link function using the R package lme4 (Bates et al. 2014). One was applied to the number of attempts per individual, the other to the number of fledglings per individual. For each model, we included state (NSW, QLD), invasion stage (front, source), year (1, 2), habitat (urban, park, edge), and tree type (native, introduced) as categorical predictors, as well as the interactions between state and habitat, invasion stage and habitat, and state and invasion stage.

Species richness (Shannon index) and the vegetation PCA scores for each of the two axes were included as a continuous predictor variables. Study site and box ID were entered as random factors.

Results Study 1

Myna abundance

To determine how frequently common mynas are in the top most abundant avian species in the largest spatial and longest temporal scale survey of the species in Australia to date, we ranked the abundances of all bird species from highest to lowest in each location where surveys took place. A comparison of the three highest abundances recorded during the two-year surveys in Queensland and New South Wales, revealed that common mynas appeared seven times in the three most abundant species, and 5/7 times in urban habitat, however this pattern was only present in New South Wales (Appendix 3).

A GLMM fitted to the myna abundances revealed that habitat was a significant predictor of common myna abundance (Table 2). The effect of habitat was qualified by state, however (Table 2), an independent samples Mann-Whitney test comparing common myna abundance in NSW with that in QLD for each habitat separately showed that mynas were significantly more abundant in urban habitat, but only in New South Wales (urban: $U=6$, $N_{(NSW)}=12$, $N_{(QLD)}=10$, $P<0.001$; Fig. 3; park: $U=64$, $N_{(NSW)}=12$, $N_{(QLD)}=10$, $P=0.821$; edge: $U=62$, $N_{(NSW)}=12$, $N_{(QLD)}=10$, $P=0.923$).

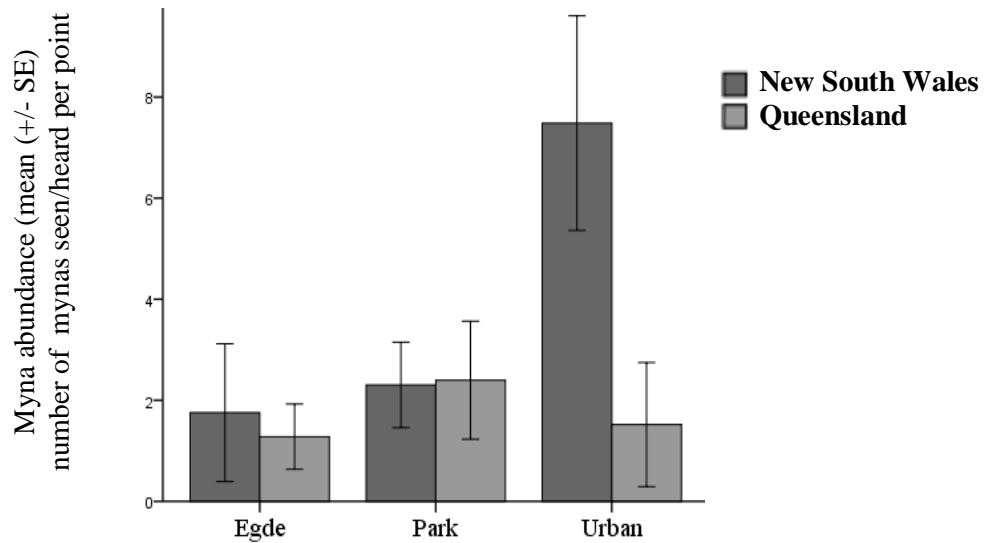


Figure 3. Myna abundances by habitat and state. At each study site (N=11, six NSW, five QLD), monthly point counts were undertaken in proximity of each array of eight nest boxes, each one of which was located in one of three habitats. For each site and each habitat, the mean number was obtained by averaging two years of monthly point counts.

The effect of habitat was also qualified by invasion stage (Table 2). The non-parametric pair comparisons Wilcoxon tests showed that common myna abundance did not follow the same pattern in source and front populations (Fig 4). On the front, common mynas were significantly more abundant only in urban habitat (urban/edge comparison $Z=5.364$, $N_{\text{urban}}=121$, $N_{\text{edge}}=122$, $P<0.001$; urban/park comparison: $Z=4.805$, $N_{\text{urban}}=121$, $N_{\text{park}}=123$, $P<0.001$; park/edge comparison: $Z=1.218$, $N_{\text{park}}=12$, $N_{\text{edge}}=10$, $P=0.223$), while on the source of the invasion they were significantly more abundant in urban and park habitat than on the edge (urban/edge comparison: $Z=6.848$, $N_{\text{urban}}=110$, $N_{\text{edge}}=111$, $P<0.001$; park/edge comparison: $Z=4.550$, $N_{\text{park}}=113$, $N_{\text{edge}}=111$, $P<0.001$; urban/park comparison: $Z=3.302$, $N_{\text{urban}}=110$, $N_{\text{park}}=113$, $P=0.001$).

Table 2. Full Poisson mixed model of the number of common mynas seen and heard per point count location

<i>Fixed parameters</i>	estimate	Std.error	t-value	<i>P</i>
(intercept)	1.334	0.668	1.996	0.045
State (Queensland)	-0.309	0.523	-0.592	0.554
Year	-0.124	0.154	-0.803	0.421
Invasion stage (Source)	-0.853	0.555	-1.536	0.124
Habitat (Park)	-0.290	0.362	-0.802	0.422
Habitat (Urban)	1.256	0.285	4.402	<0.001
Species richness	-0.288	0.249	-1.156	0.247
State* invasion stage (QLD*Source)	0.585	0.558	1.048	0.294
State*Habitat (QLD*Park)	0.243	0.561	-0.434	0.664
State*Habitat (QLD*Urban)	-1.662	0.537	-3.090	0.002
Invasion stage*Habitat (Source*Park)	1.397	0.545	2.560	0.010
Invasion stage*Habitat (Source*Urban)	0.697	0.514	1.356	0.175
<i>Random effect</i>	Variance	sdt.dev		
Study site	0.083	0.289		

Reference categories of categorical variables are noted between brackets beside the variable name. Bolded p-values were below a 0.05 threshold of significance.

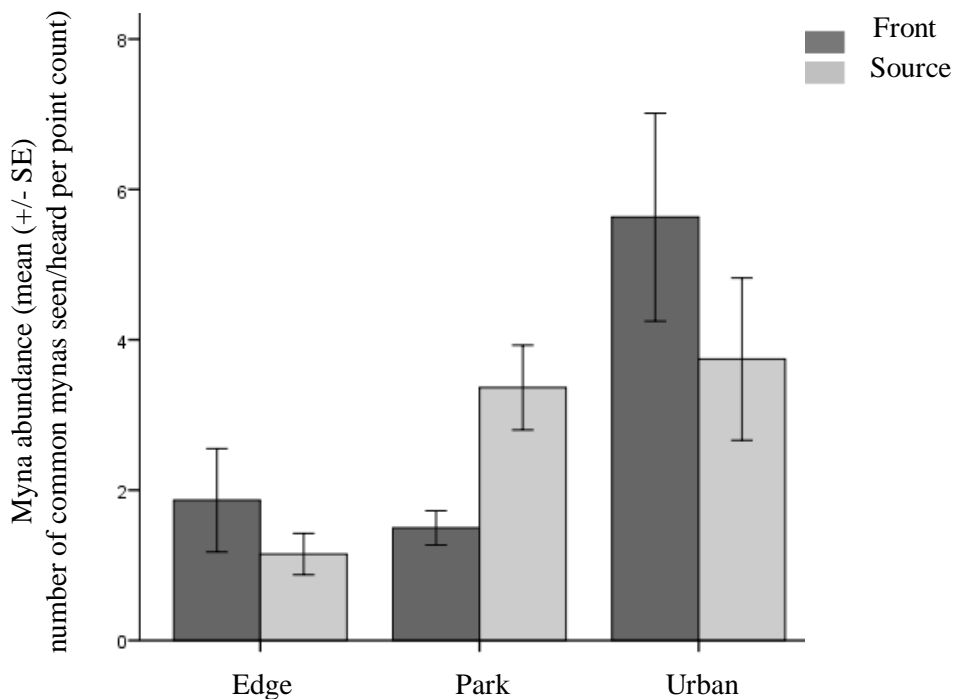


Figure 4. Myna abundances by habitat and myna invasion stage. At each study site (N=11, six front, five source), monthly point counts were undertaken in proximity of each array of eight nest boxes, each one of which was located in one of three habitats. For each site and each habitat, the mean number was obtained by averaging two years of monthly point counts.

Myna nest box occupancy

During the first year of the study, nest box occupancy by birds was 29.1% in NSW and 13.3% in QLD. During the second year of the study, nest box occupancy in NSW remained approximately similar (29.9%), whereas it increased slightly in QLD (16.7%). In both states, the most common avian occupants of the boxes were the introduced common myna and a collection of native parrot species of similar body size. Statistical analyses revealed that habitat was the significant predictor of common myna nest box occupancy (Table 3). Common mynas occupied significantly more nest boxes in urban habitat than in edge habitat (Fig. 5).

Table 3. Full zero-inflated Poisson mixed model of the number of boxes occupied by mynas

Fixed parameters	Estimate	Std.Error	Z	P
Intercept	1.678e+00	4.549e+00	0.369	0.712
State (QLD)	-2.333e+01	3.928e+04	-0.001	0.999
Invasion stage(Source)	1.762e-04	8.968e-01	0.000	0.999
Year	-5.649e-01	3.566e-01	-1.584	0.113
Habitat (Park)	4.230e-01	7.750e-01	0.546	0.585
Habitat (Urban)	1.366e+00	6.714e-01	2.034	0.041
Species richness	-7.156e-01	1.465e+00	-0.488	0.625
State* Invasion stage	2.382e+01	3.928e+04	0.001	0.999
(QLD*Source)	-1.284e-01	1.006e+00	-0.128	0.898
State*Habitat (QLD*Park)	-5.306e-01	1.216e+00	-0.436	0.662
State*Habitat (QLD*Urban)				
Random effect	Variance	sdt.dev		
Study sites	1.012e-08	0.0001		

Reference categories of categorical variables are noted between brackets beside the variable name. Bolded p-values were below a 0.05 threshold of significance.

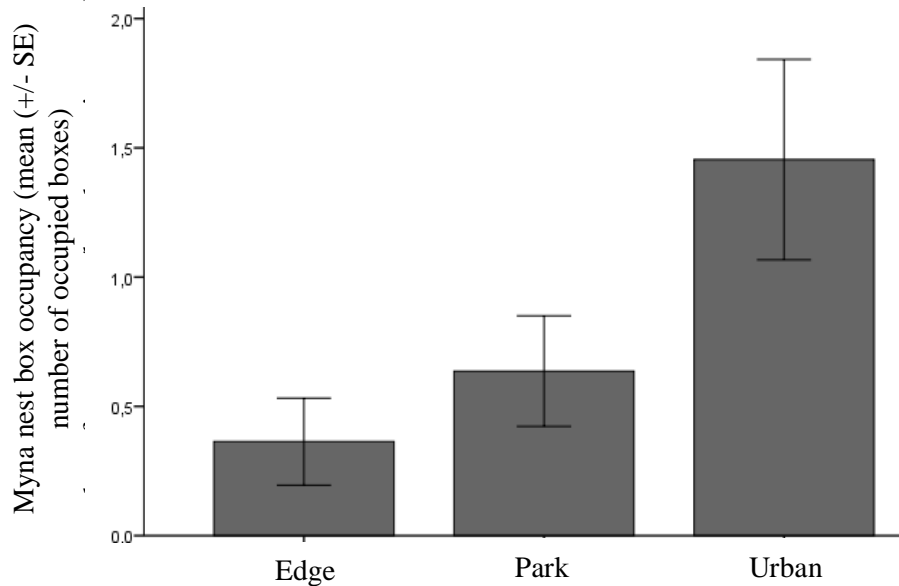


Figure 5. Myna nest box occupancy by habitat. In each study site (N=11), eight nest boxes were located in each of three habitats (edge, park, urban; total 88 nest boxes per habitat). Nest box occupancy was recorded weekly for two successive breeding seasons. For each habitat, the mean number of occupied boxes was obtained by averaging two years of monitoring data across eleven study sites.

Nesting attempts and breeding success of mynas

Despite the intensive sampling effort and scale of our study (264 nest boxes monitored weekly for two successive breeding seasons across two states and three habitats), we were not able to identify any significant predictors of the extent to which mynas tried to use our nest boxes (i.e. laid at least one egg), or the extent to which they succeeded in fledging young from our nest boxes. None of the explanatory variables considered in our statistical models predicted the extent to which mynas attempted to breed (Table 4), or their fledgling success (Table 5).

Table 4. Full Poisson GLMM on number of common myna nesting attempts by nest box

<i>Fixed parameters</i>	Estimate	Std.Error	Z	P
intercept	2.024	2.265	0.894	0.372
State (QLD)	-0.239	0.546	-0.438	0.661
Invasion stage (Source)	0.333	0.836	0.398	0.690
Habitat (Park)	-0.570	0.793	-0.719	0.472
Habitat (Urban)	-0.082	0.689	-0.120	0.904
Year	-0.127	0.206	-0.615	0.539
Tree (non-native)	0.173	0.406	0.427	0.669
Species richness	-0.634	0.798	-0.795	0.427
PC1 (Seal ground)	0.136	0.144	0.943	0.345
PC2 (Shrub)	-0.041	0.226	-0.185	0.853
Stage*Habitat (Source*Urban)	-0.317	0.896	-0.353	0.724
State*Habitat (QLD*Park)	0.114	0.760	0.151	0.880
<i>Random factors</i>	Variance	sdt.dev		
Box ID	0	0		
Study site	0	0		

Reference categories of categorical variables are noted between brackets beside the variable name.

Table 5. Full Poisson GLMM on number of fledglings per individual in common mynas

<i>Fixed parameters</i>	Estimate	Std.Error	Z	P
intercept	0.531	3.880	0.137	0.891
State (QLD)	0.529	0.708	0.747	0.455
Invasion stage (Source)	-1.039	0.958	-1.084	0.278
Habitat (Park)	0.134	1.068	0.126	0.900
Habitat (Urban)	-0.608	0.751	-0.809	0.418
Year	-0.261	0.293	-0.892	0.373
Tree (non-native)	-0.148	0.509	-0.292	0.770
Species richness	-0.077	1.385	-0.056	0.955
PC1 (Seal ground)	0.079	0.186	0.425	0.671
PC2 (Shrub)	0.058	0.287	0.204	0.838
Stage*Habitat (Source*Urban)	0.947	1.195	0.793	0.428
State*Habitat (QLD*Park)	-0.689	1.054	-0.654	0.513
<i>Random factors</i>	Variance	sdt.dev		
Box ID	0.000	0.000		
Study site	0.000	0.000		

Reference categories of categorical variables are noted between brackets beside the variable name

Study 2

Aims Study 2

Study 1 failed to reveal any significant predictors of myna breeding. Study 2, just like Study 1, aimed to determine, but using a slightly modified experimental design, whether mynas show changes along an invasion wave in their tendency to occupy and breed in urban environments preferentially. Relative to Study 1, Study 2 provided a geographically more local (Hunter region, see below), but temporally longer (three vs. two years) and more powerful (number of source nest boxes augmented) analysis of myna breeding across an invasion wave. Just like in Study 1, we studied mynas across three different habitats, namely urban, park and edge. Given that native secondary cavity nesting parrots were the other most common occupant of our nest boxes and are reported to suffer heavily from myna competition over limited nesting resources (Tidemann et al. 2011), we took the opportunity to expand our taxonomic scope to include a comparison of breeding in common mynas and native parrots along the invasion wave. Study 2 had the same predictions as Study 1 in regard to the potentially interacting effects of habitat and invasion stage on myna nest box occupancy and breeding behaviour. Based on existing research, we also predicted that mynas would show greater nest-box occupancy and fledgling success than native parrots in source and urban habitats in both invasion front and invasions source populations of mynas.

Methods Study 2

Study sites, nest boxes, nest box monitoring

The study sites for Study 2 were four of the NSW study sites sampled in Study 1 (two front, two source, total 96 nest boxes), augmented by an additional 30 nest boxes installed in three additional source sites in the larger Newcastle area (Fig. 6, appendix

1&2). The geographical area covered by the nest boxes used in present study (total 126 nest boxes, 48 front, 78 source) is generally referred to as the Hunter Valley region. All nest boxes were identical in design to those of Study 1, and were monitored using the same weekly protocol, recording species ownership, the number of nesting attempts (i.e. at least one egg laid), and the number of eggs, nestlings and fledglings for each clutch. In sum, Study 2, while being geographically more localized, increased the duration of monitoring from a two year to a three year period and nearly doubled the sampling effort at NSW source sites (48 boxes in Study 1 vs. 78 boxes in Study 2).

All procedures were approved by the animal ethics committee of the University of Newcastle (ARA A-2014-424).

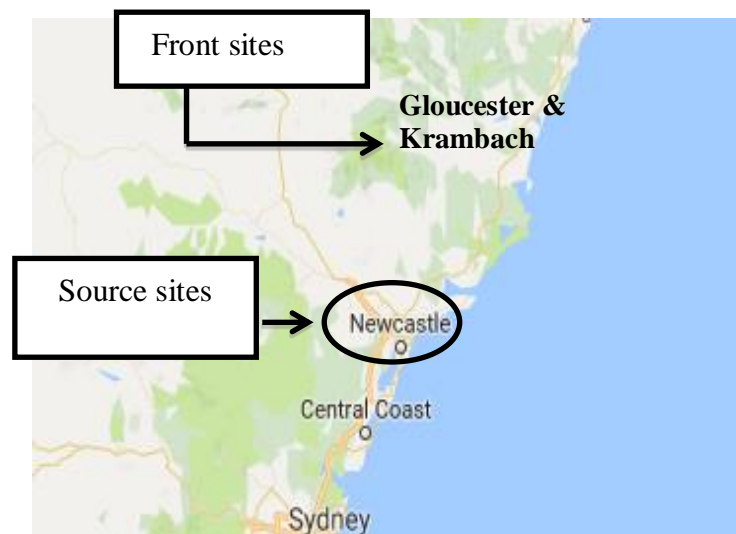


Figure 6. Locations of NSW study sites for Study 2. An array of 24 nest boxes was located in each of two NSW front sites. These boxes were the same as those used in Study 1. An array of 24 nests boxes was located in each of two source sites within the larger Newcastle area. These boxes were also identical to those used in Study 1. This array of 96 boxes was augmented by thirty nest boxes distributed in three additional source study sites located in source sites in the larger Newcastle region.

Data analysis

Study 1 included the monitoring data from two successive myna breeding seasons on an array of 96 NSW nest boxes. In Study 2, we added to this data set an additional year of

monitoring data for the same nest box array, totalling three years of monitoring data. We also added to the Study 1 data set three years of nest box breeding data collected on an additional 30 nest boxes installed in NSW source sites (Fig. 6; appendix 2). In addition, rather than focusing on explaining myna breeding only, we expanded the taxonomic scope of the study to include both myna and native parrot breeding data.

Nest box occupancy

We calculated the number of nest boxes (max=12) occupied by common mynas in each site and habitat. This variable was used as an outcome variable in a zero-inflated negative Poisson mixed model with a log link function using the R package glmmTMB (Brooks et al. 2017). This model was selected to take into account simultaneously the high proportion of zeros (sites where no box was used by common mynas or native parrots) and the over-dispersion of the data around zero (Zuur et al. 2009). We included species (parrot sp./myna); invasion stage (front, source), year (1, 2, 3), and habitat (urban, park, edge) as categorical predictors, as well as the interactions between species and habitat, species and invasion stage, and species and year. Study site was included as random factor.

Breeding success in mynas versus native parrots

As for Study 1, under the assumption that the total number of fledglings recorded in each nest box for each year of the study was produced by the same pair (for mynas and native parrots, respectively), we calculated, for each box, each species (myna, native parrot), and each year of the study, the total number of fledglings per individual by dividing by two the total number of fledglings recorded in a nest box for each breeding season. We used this variable as a measure of breeding success, to which we fitted a Poisson (GLMM) with a log link function using the R package lme4 (Bates et al. 2014). We included species (parrot sp./myna), myna invasion stage (front, source), year (1, 2,

3), and habitat (urban, park, edge) as categorical predictors, as well as all 2-way interactions involving species. We included study site and box ID as random factors.

Results Study 2

Nest box occupancy by mynas and native parrots

The overall nest box occupancy increased across the three years of the study from 23.0% in year 1, 30.2% in year 2 to 32.5% in year 3 (Table 6). The mean level of nest box occupancy for common mynas across the three years was 44.8% and 55.2% for native parrots (Table 6). Eastern rosellas were by far the most common native parrot found to be nesting in the nest boxes (Table 6). Invasion stage was the only predictor of nest box occupancy (Table 7). The source sites exhibited a higher rate of occupancy in comparison with front sites (Fig 7).

Table 6. Comparison of nest box occupancy and breeding success of common mynas and native parrots across three breeding seasons in the Hunter valley in Study 2.

Breeding season	Species	% of occupied boxes	Number of attempts	Number of eggs	Number of fledglings	Number of fledglings per individual
1	Common mynas	48.28	17	68	15	0.54
	native parrots ¹	51.72	16	63	10	0.33
2	common mynas	42.11	26	102	50	1.47
	native parrots ²	57.89	28	130	25	0.54
3	common mynas	43.90	29	119	42	1.11
	native parrots ³	56.10	24	105	38	0.83

¹11 boxes occupied by eastern rosellas, 3 by crimson rosellas and 1 by rainbow lorikeets (*Trichoglossus moluccanus*)

²20 boxes occupied by eastern rosellas, 1 by crimson rosellas and 2 by rainbow lorikeets

³21 boxes occupied by eastern rosellas, 1 by crimson rosellas and 1 by rainbow lorikeet

Table 7. Full zero-inflated Poisson mixed model of the number of boxes occupied as a function of species (native parrot /myna), myna invasion stage, habitat, and year

<i>Fixed parameters</i>	Estimate	Std. Error	Z	P
Intercept	-21.617	10308.812	-0.002	0.998
Species (Native parrots)	20.818	10308.813	0.002	0.998
Invasion stage(Source)	1.687	0.700	2.410	0.015
Year2	0.143	0.380	0.379	0.704
Year3	0.327	0.365	0.897	0.369
Habitat (Park)	20.883	10308.812	0.002	0.998
Habitat (Urban)	21.274	10308.812	0.002	0.998
Species*Year (Native parrots*Year2)	-0.359	0.579	-0.620	0.535
Species*Year (Native parrots*Year3)	-0.4279	0.555	-0.770	0.441
Species*Habitat (Native parrots*Park)	-19.851	10308.813	-0.002	0.998
Species*habitat (Native parrots*Urban)	-19.943	10308.812	-0.002	0.998
Species*Invasion stage (Native parrots*Source)	-0.637	0.630	-1.011	0.311
<i>Random effect</i>	Variance	Std.Dev.		
Site	0.2745	0.5239		

Reference categories of categorical variables are noted between brackets beside the variable name. Bolded p-values were below a significance threshold of 0.05.

Myna versus native parrot breeding success

Common mynas fledged on average 1.06 ± 0.15 SE chicks/individual across the three breeding seasons. This rate was twice as high as for native parrots, which fledged on average 0.59 ± 0.87 SE chicks/individual (Table 6). However, over the years, species failed to predict breeding success (Table 8). Statistical analyses on the number of fledglings per individual revealed that year was a significant predictor of breeding success (Table 8). Breeding in Year 2 was significantly higher than in Year 1 for both native parrots and common mynas.

Table 8. Full Poisson GLMM on number of fledglings per individual as a function of species (native parrot sp/myna), myna invasion stage, habitat, and year.

<i>Fixed parameters</i>	Estimate	Std.Error	Z	P
Intercept	-1.716	1.254	-1.368	0.171
Species (Native parrots)	-0.253	0.702	-0.360	0.718
Invasion stage (Source)	-0.219	0.601	-0.364	0.716
Habitat (Park)	2.198	1.175	1.870	0.061
Habitat (Urban)	1.745	1.132	1.541	0.123
Year2	0.674	0.343	1.961	0.049
Year 3	0.516	0.346	1.493	0.135
Species*Year (Native parrots*Year2)	-0.235	0.561	-0.419	0.675
Species*Year (Native parrots*Year3)	0.204	0.535	0.382	0.702
Species*Invasion stage (Native parrot*Source)	0.042	0.706	0.060	0.952
Species*Habitat (Native parrots*Park)	-0.558	0.486	-1.149	0.250
<i>Random effects</i>	Variance	sdt.dev		
Box ID	0.410	0.6407		
Study sites	0.0001	0.0111		

Monitoring data were collected in the Hunter Valley region across three breeding seasons. Reference categories of categorical variables are noted between brackets beside the variable name. Bolded p-values were below a significance threshold of 0.05.

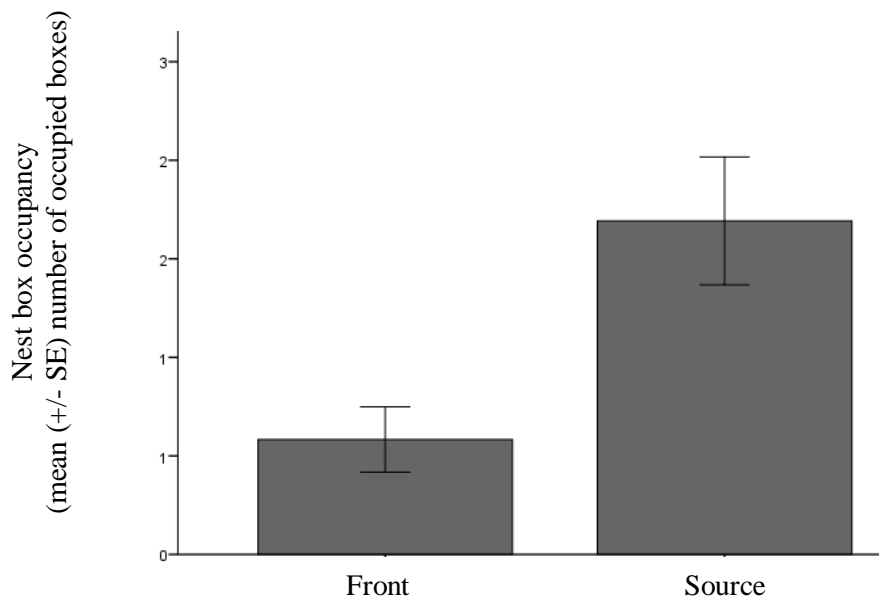


Figure 7. Nest box occupancy pooled across native parrots and non-native common mynas by myna invasion stage. In each study site (N=7), the mean number of occupied boxes was obtained by averaging three years of weekly monitoring data.

Discussion

The work presented here explores for the first time abundance and breeding success of common mynas in relation to habitat and invasion stage (front/source) over several breeding seasons and across two Australian states (New South Wales and Queensland). Our experimental design, using a large array of nest boxes within both states, allowed us to replicate study sites and investigate two invasion waves for the first time simultaneously.

According to our predictions, which were based on several previous analyses of common myna distribution across habitats in NSW, Victoria and Australian Capital Territory (ACT) (Crisp & Lill 2006; Grarock et al. 2014; Haythorpe et al. 2013; Sol et al. 2012), mynas should have been most abundant in urban environments. However, results revealed that NSW and QLD exhibited different patterns of habitat selectivity. In NSW, common mynas were significantly more abundant in urban habitats while no difference in abundance was found between urban (impervious), park and edge habitats in QLD. This surprising difference in habitat specificity across two separate invasion waves could reflect a lower tendency for southern Queensland mynas to prefer urban habitats. Introduction history and population genetics differ between central NSW and southern QLD (Ewart et al. in review). Whereas central NSW mynas represent a range expansion of (likely) overseas birds introduced to Sydney (Hone 1976; Long 1981), recent genetic analyses have revealed that southern QLD birds form a distinct genetic cluster possibly originating from northern QLD birds, which themselves originated from Melbourne birds translocated to cane fields in north QLD to combat locusts and cane beetles (Chisholm 1919; Long 1981; Ewart et al. in review). This history of translocation to cane fields prior to translocation to southern QLD could have produced a southern QLD genetic cluster with a lower habitat preference for cities.

Source and front populations across both states also displayed variation in habitat specificity. Common mynas were more abundant in urban areas and parks in source populations while in the front, they were more abundant in urban areas but not in parks. This distinct pattern of habitat occupation across source and front populations could reflect the dynamics of range expansion across time and space: as highly urbanized source birds increase in density, competition for food and nesting sites (Shochat 2016) increases. With time, individuals with a reduced preference for urban environments overflow into patches of less urban habitat within cities (e.g. parks), sub-urban areas on the periphery of cities, and range expand into smaller, more rural townships on the invasion front (www.feralscan.org.au/mynascan). Individuals that are less competitive and ill-equipped to deal with urban habitats, due to high neophobia for example (see chapter 2), might be more prone to travelling greater distances. Those less competitive individuals, for example birds that do not have access to enough insects and rely only on anthropogenic food could be pushed away by more competitive ones. An experimental study in Sydney has showed that birds fight over food items with high level of proteins demonstrating how this type of food intake is important in urban common mynas (Machovsky-Capuska et al. 2015). Therefore, individuals that could not successively compete over such important resource might have to seek further and move to more sub-urban or rural habitats where insects are more numerous. Although the pattern of habitat distribution found here indicates the front mynas colonise front urban habitats first, these urban environments are only urban at a local scale. At a larger scale, due to the small size of townships on the invasion front, front habitats are less urban.

In addition to this phenomenon, city centers in Australia have changed over time. Human population in major capital cities has grown 60.6% from 1911 to 2006 and 35% in regional towns and cities, according to the Australian census of 2006

(Department of Infrastructure, Regional Development and Cities of Australia, report 136). This continuous explosion of human population in urban centers provides a profusion of human refuse which represents an opportunity for predictable food resources for common mynas. Yet in parallel to this growing urbanisation and human presence, the number of insects, an essential food item to feed common myna nestlings, is drastically decreasing (Jones & Leather 2012; Rocha et al. 2018). Cities hence represent immense opportunities for mynas by presenting large amounts of anthropogenic food, but they may also represent a trap in which the insects may be too scarce to adequately feed hatchlings and thus where breeding could be compromised. Additionally, the architecture of CBD (central business district), the heart of cities have changed, less trees and more glasses. Urban studies in avian populations mostly occurred in parks and green spaces, a recent evaluation of building use by urban commensal avifauna in Melbourne central business district (Pike et al. 2017) discovered that the architectural period of the building was a determinant factor of bird presence with feral pigeons (*Columba livia*), house sparrows (*Passer domesticus*) and common mynas mostly found on historic buildings. Although the present study did not reveal any difference in breeding success across habitats, longer term work (10/15 years) investigating lifetime reproductive success along an urban gradient might find evidence for such a difference.

As predicted, nest box occupancy by common mynas paralleled their abundance and decreased as urbanisation decreased. However, neither habitat nor invasion stage predicted the breeding success in common mynas. This finding confirms those of a previous study in Canberra, ACT, whereby decreases in urbanisation from high to medium tree cover predicted decreases in abundance and nest box occupancy, but did not reveal a decrease in breeding success (Grarock et al. 2013). This provides

convergent evidence that, although common mynas appear to prefer to occupy and breed in urbanized habitats, they are equally successful in breeding in less urban ones. Hence, assuming similar demographics as in high levels of urbanisation, medium levels of urbanisation are therefore unlikely to offer a barrier to the range expansion of the species once it has successfully colonized these habitats. This is in line with observations that the myna is not a strong habitat specialist and has the capacity to occupy a range of environments (Counsilman 1974; Crisp & Lill 2006).

The second study, limited to the New South Wales invasion wave, revealed that over three years of records, nest box occupancy and breeding success had similar levels in native parrots and the introduced common myna. The only predictor of nest box occupancy was invasion stage, with source populations having higher nest box occupancies than front populations. It is not clear why nest box occupancy in mynas is greater in source populations than in front populations, given that source populations were not overall more abundant than front populations, yet prior work has demonstrated strong correlations between abundance and nest box occupancy. Further research is required to determine whether higher nest box occupancy in source populations, for both mynas and parrots, is due to lower availability of natural cavities given the tendency for source areas to be more urban at large scales of analysis.

The only predictor of breeding success was the year of breeding both in native parrots and the common myna. Despite common mynas showing a high, and parrots showing a very low, breeding success in Year 1, this taxonomic difference disappeared across the years. One possible explanation is that the nest boxes were colonized initially by young, inexperienced pairs of parrots, which gradually improved their breeding experience across the years. Fidelity to nesting sites, especially after successful breeding, has been showed in parrots (Salinas-Melgoza et al. 2009) and in many other

bird species such as eastern bluebirds (*Sialia sialis*) (Stanback & Dervan 2001), American robins (*Turdus migratorius*) and brown thrashers (*Toxostoma rufum*) (Haas 1998). Fidelity to nesting site, but also age is a determining factor of breeding success, older (experimented) pairs undergo an higher breeding success than young pairs (Forslund & Pärt 1995; Rebke et al. 2010; Riechert et al. 2012). However this pattern is strongly entangle with food availability (Furness 2015; Ratcliffe et al. 1998) and differences over the years of breeding success could also be a direct consequence of different annual levels of food quality or availability. Those findings underline the fact that parenting and foraging skills are similarly important to breeding success. By leaving nest boxes in place for several years, the capacity to support the breeding of native parrots may improve. This provides interesting opportunities for urban nest box programs.

Nest boxes can thus support the presence of native secondary cavity nesting birds in urban areas, as long as they are left in place for long enough. Boosting native cavity-nesting parrot breeding might help boost their abundances in our cities, and perhaps, with it, their capacity to compete with mynas. Indeed, informally, the present study revealed that parrot pairs tended to nest in groups of nearby nest boxes, with no spatial overlap with breeding mynas even though mynas foraged on the ground nearby, suggesting that agglomerations of parrots can exclude mynas from breeding resources.

In conclusion, the present study of common myna distribution and breeding success as a function habitat and invasion stage revealed that common mynas might vary in their levels of preference for urban habitat across different invasion waves, but also with time since establishment, with mynas spreading from an urban core to less urban patches as abundances increase. Breeding success does not appear to be affected by habitat type, however. It is possible that variation in habitat preferences allows the

myna to spatially segregate across qualitatively different habitats, facilitating its range expansion from large city centers to smaller, more rural, ones. The study also showed that nest boxes programs have promising potential in promoting native bird species breeding in urban environments, but need to be managed carefully to reduce occupation by mynas. Temporarily closing nest boxes during peak myna breeding time (December-February) and opening them during peak parrot breeding time (September-November) might provide a useful management strategy.

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Final discussion

This thesis advances our knowledge of common myna ecology and behaviour and furthers our understanding of the factors explaining the spread of invasive species. This work is the first to have simultaneously investigated the morphology, the ecology and the behavioural traits of common mynas. Most importantly, this body of work is the first to explore potential differences between populations of myna birds at different stages of the invasion process.

Common mynas exhibited differences as a function of the invasive stage. At the front of the invasion, common mynas exhibited longer beaks, better health and a higher level of neophobia than their counterparts in old-established populations. We found differences in abundance and nesting site (nest boxes) occupancy. These differences varied between Queensland and New South Wales, between old and recently-established common myna populations and between habitats.

In this work I have found little evidence of common mynas outcompeting native species over nesting sites. However, an experiment involving the noisy miner (an aggressive native species) revealed that this honeyeater displayed a high level of aggressiveness towards common mynas and could contribute to their range expansion.

1. Do common mynas outcompete with native species?

Common mynas are often referred to as ‘highly aggressive’ especially towards native species when competing for nesting sites (Pell & Tidemann 1997). Their ability to outcompete native cavity-nesters, sometimes by going as far as killing them has been the main argument used to explain their high breeding success and the decline of some

native species. Three years of close monitoring of over a large array of nest boxes across two states has revealed no take over from the invasive species in direction of native parrots. One caveat of our study design is that it takes place in somewhat urbanized habitats. Nesting sites are commonly described as a scarce resource in urban areas (Shochat et al. 2010). The addition of nest boxes might have increased the number of nesting opportunities in a given area to a point where cavities were no longer the limiting factor and therefore might reduce the competition. However our results are in line with a growing number of publications that after looking at common myna behaviour, suggest that this species may have little impact on native wildlife in Australia (Haythorpe et al. 2012; Lowe et al. 2011; Parsons et al. 2006) contrary to what was thought before (Pell & Tidemann 1997).

Beyond displacing and performing aggressive interactions towards native species, mynas can also outcompete them by being more ecologically successful in their environment. Our study of common myna nesting behaviour shows that their high breeding success might be due to the quality of their parental care. For the first time, the time spent at nest and the number of nest intruders (other birds and all type of predators) was recorded in common mynas and eastern rosellas (main other cavity nester in nest boxes). This showed that common myna parents were four time more present at nest than eastern rosella parents and underwent less nest intrusions from other birds and predators. This corresponds to the strict dietary requirements of myna hatchlings which require an insect-exclusive diet for their two first weeks of life. Parents must hence move back and forth from nest to foraging sites all day long. On the other hand rosella chicks are fed from many different food items which parents may need to collect in large quantities before regurgitating. The high presence of mynas at their nest may enable a better surveillance and protection from competitors and predators. In addition

to their presence at the nest, common mynas are a very vocal song bird that displays a number of different vocalisations (Counsilman 1974), and can even perform mimicking (Soomro & Narejo 2016). In this way, parents are not only visually present, but also acoustically present at the nest. This high level of presence may protect them from other species taking over their nest or from predation, and consequently could improve their level of breeding success.

2. Factors and mechanisms associated with the range expansion of common mynas

All studies presented in this thesis investigated potential differences in common myna populations at the two extremes of the invasion wave. To understand which factors could drive the range expansion of common mynas in Australia, I developed my research following three axes: myna morphology and health, myna social and novelty-related behaviours, and noisy miner responses to intruders including mynas. First, I examined morphological and health differences in old and recently-established populations of common mynas and discovered common mynas have different diets and beak length, and are of better health on the invasion front than in old-established populations. These findings suggest that habitat, especially urbanization, could drive the common myna range expansion. Common myna are first attracted to urban habitat by the abundant predictable anthropogenic food, but when bird density grows, this habitat poor in arthropods and insects may do not provide enough adequate food items to rise healthy nestlings. Therefore, some individuals could spread towards suburban areas or towards the front of the invasion. Second, when I compared the levels of sociality and neophobia in source and front populations of juvenile common mynas I found that birds on the front of the invasion exhibited a higher level of neophobia and discussed how

this behaviour could be involved in a mechanism driving the range expansion. Then, I investigated the noisy miner agonistic interactions towards different types of intruders on their territories,

This work demonstrated that noisy miner aggression was only directed towards species with which they overlap and with which they are already familiar. In other words, the noisy miners must be sympatric with the common myna for a certain period before becoming aggressive towards it. Under these conditions, this native bird could be a driver of the common myna spread instead of being a biotic barrier. By harassing the common mynas in old-established populations where they have co-occurred for a significant period of time and chasing them further away, the noisy miner could contribute driving the common myna range expansion. Finally, a long term study of common myna abundances and breeding success revealed some geographical differences across the invasive range in abundance but not on breeding success, suggesting that common mynas have developed an attraction to urban areas but they are able to shift this preference towards other habitat when necessary (e.g. for higher quality foraging territories) without any consequences on their breeding success.

Taken together these results allow me to propose an outline of the mechanisms that might drive the common myna ongoing invasion in Australia (Fig 1). Behaviour, habitat and species interactions seem to play an important role in the spread of common mynas in Australia. The final stage of the invasion process (the spread) must be seen as a result of interacting factors. While our studies explore only a few factors involved in common myna expansion, this work underlines the importance of looking at potential explanatory factors together instead of looking at each factor in isolation.

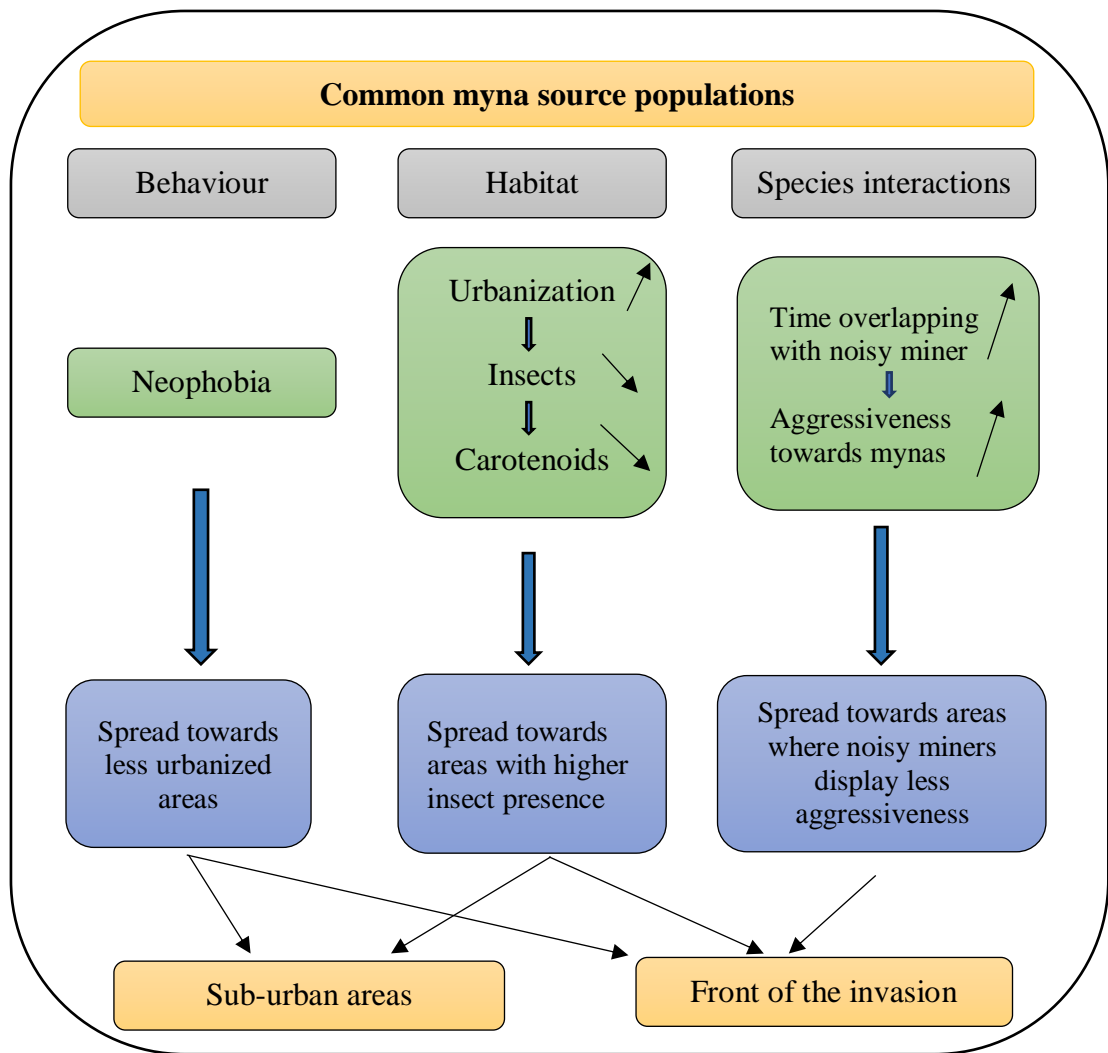


Figure 1. An outline of the factors and mechanisms driving the spread of common myna to novel areas in Australia (front of the invasion) and to novel habitats (sub-urban areas).

3. Management and conservation implications

Our study across Queensland and New South Wales (Chapter 5) showed disparities in common myna abundance across states, habitats and stages of the invasion. Historically common mynas in Australia are particularly successful in urban areas (Sol et al. 2012). We did confirm this trend, showing that common mynas are more abundant in urban habitat but only in NSW and not in Queensland. Additionally, in long-established populations, the park habitat showed a higher abundance of common mynas than in front populations. These geographical discrepancies emphasize the importance of using

data-driven decisions to perform management, and in particular in the case of trapping programs. A coordination within states should help to target the locations with highest common myna densities. The diminution and the control of bird numbers in those areas should help to limit the spread of individuals towards locations where less density occur.

However, we demonstrated that common mynas have the potential to switch their habitat preference (urban habitat) and are able to breed successfully in less urbanised habitat as well. Consequently, targeting control programs to some areas or type of habitat could not be efficient enough. Developing contraception programs to limit common myna abundance in urban areas might be more efficient in the long term. Of course, contraception programs could lead to create a sink and attract populations from sub-urban areas and incite suburban birds to invest urban centers. However, on long term, these programs will also impact those populations. Keeping low densities in urbanised areas could reverse the spiral and the direction of the expansion. Instead of moving from urban centers towards sub-urban areas and more rural townships, low densities in highly urbanised areas might attract birds to places where contraception programs would control their number, stop the spread in direction of novel areas.

Our large sample of nest boxes across New South Wales over three breeding seasons provided a very useful tool to estimate breeding success in native and invasive species. Nest box occupancy was similar in native parrots and common mynas. While common mynas displayed a higher rate of breeding success the first year, over the years, the gap between common mynas and native parrots breeding success reduced. After three years, native parrot breeding success was equivalent to that of common mynas. This result demonstrates that nest box programs could be beneficial to native wildlife even in the presence of the invasive common myna, in particular if such programs are

continued over a long time during which native parrots can improve their success with the devices.

Close monitoring of the nest boxes revealed a slight difference between common mynas and native parrots in the period and length of their breeding season. Some eastern rosellas started laying eggs the last week of August and the last fledglings left the nest early January while common myna first eggs appeared late September and the last chicks fledged in April. This difference offers interesting opportunities in terms of management. For example, one could apply a lid on the nest box entrances in mid-January which could prevent common mynas from laying their second or third clutch without disturbing eastern rosellas. Citizens, especially in cities, show more and more interest in biodiversity and wildlife. Using the results described above and previous knowledge in common mynas, it is possible to undertake nest box programs such that our cities become wildlife-friendly.

4. Limitations and future research

One limitation of this body of work is related to the shape of the common myna invasion wave. In each study, I selected carefully study and/or trapping sites and tried to match them as closely as possible in source and front locations. Because the invasion is going westward from large urban centers towards smaller cities centers, when looking at a larger scale birds on the front of the invasion lived in less urbanised areas, even though, at a small scale, front and source mynas were captured in habitats of similar urbanization levels. Under these conditions, it is difficult to disentangle the relative importance of large scale habitat and of stage of invasion in the differences found in front and source bird populations.

As it was demonstrated in this thesis, several factors influence the mechanisms driving the invasion process. However not all of them have been subject to investigation in this body of work. Other ecological factors such as predation pressure, climate (global warming) and other behavioural traits (e.g. exploration) could also be taken into consideration. Future research may follow the approach developed here and try to overcome the limitations described above. For example, additional comparisons between rural populations in old and recently-established populations could help to tease apart the respective importance of habitat and of the invasion stage.

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Appendix 1

Nest box locations in New South Wales

- 2 source sites in Newcastle area (New Lambton, Glendale)
- 4 front sites (Gloucester, Krambach, Tamworth, Armidale)

Each site was divided in three type of habitat: urban, park and edge of the bush.

8 nest boxes per habitat

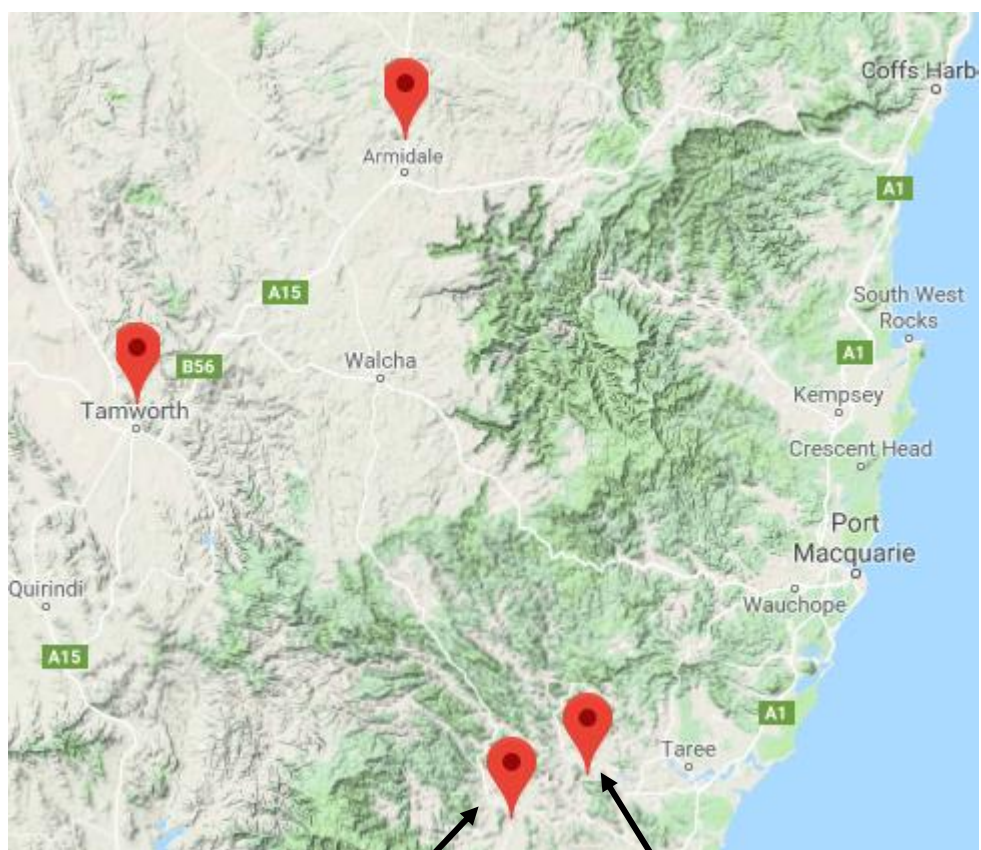
24 nest boxes per site

192 nest boxes in NSW





Source sites Newcastle area



Gloucester

Krambach

4 Front sites

1. source site New Lambton

New Lambton nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude
60	Edge	-32,932375	151,70303
63	Edge	-32,932276	151,7031
64	Edge	-32,932195	151,703315
65	Edge	-32,932496	151,702896
66	Edge	-32,932393	151,702537
68	Edge	-32,932794	151,701711
71	Edge	-32,932569	151,703856
72	Edge	-32,932298	151,70354
49	Park	-32,931976	151,70827
50	Park	-32,931857	151,708254
54	Park	-32,932312	151,70812
55	Park	-32,932179	151,708367
56	Park	-32,932758	151,708133
57	Park	-32,932611	151,708058
58	Park	-32,931739	151,708582
59	Park	-32,931704	151,708404
51	Urban	-32,934665	151,707204
52	Urban	-32,933515	151,707417
53	Urban	-32,934156	151,707321
61	Urban	-32,934291	151,707299
62	Urban	-32,934453	151,707251
67	Urban	-32,933753	151,707409
69	Urban	-32,934471	151,707032
70	Urban	-32,934794	151,70718



New Lambton three habitats



2. Source site Glendale

Glendale nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude
89	Edge	-32,931151	151,63903
90	Edge	-32,931007	151,6389
91	Edge	-32,930976	151,63873
92	Edge	-32,930854	151,63868
93	Edge	-32,930834	151,63848
94	Edge	-32,930667	151,63865
95	Edge	-32,930672	151,63845
96	Edge	-32,930561	151,63838
73	Park	Glendale three habitats	
74	Park	-----	
78	Park	-32,929492	151,6393
79	Park	-32,928718	151,63944
80	Park	-32,929096	151,63969
81	Park	-32,929006	151,63962
87	Park	-32,929166	151,63948
88	Park	-32,928778	151,63991
75	Urban	-32,928185	151,64864
76	Urban	-32,927744	151,64857
77	Urban	-32,928001	151,64863
82	Urban	-32,929457	151,6488
83	Urban	-32,928928	151,64875
84	Urban	-32,929156	151,64878
85	Urban	-32,928692	151,64875
86	Urban	-32,928473	151,64868

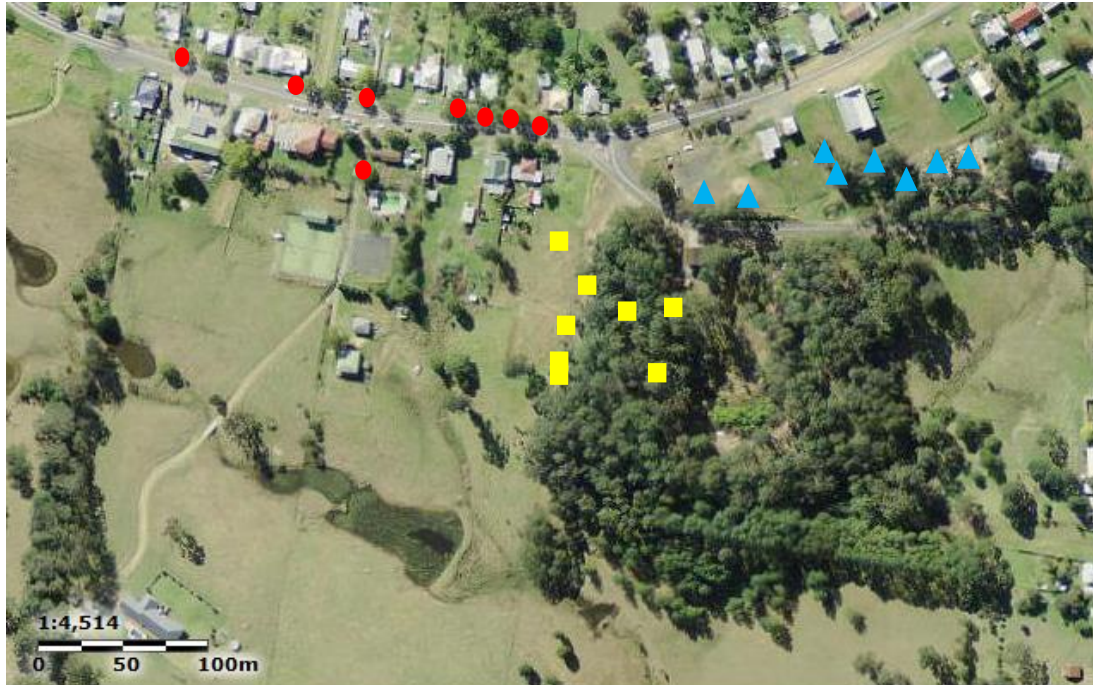
3. Front site Gloucester



Gloucester three habitats

Gloucester nest box GPS coordinates							
Box ID	Habitat	Latitude	Longitude	Box ID	Habitat	Latitude	Longitude
17	Edge	-32,00611	151,95216	1	Urban	-32,01086	151,95989
18	Edge	32° 0'21.32"S	151°57'8.19"E	2	Urban	-32,01116	151,95983
19	Edge	-32,00571	151,95231	3	Urban	-32,01175	-32,011973
20	Edge	-32,0057	151,95243	4	Urban	-32,01205	-32,011956
21	Edge	-32,00587	151,9526	5	Urban	-32,01254	-32,011934
22	Edge	-32,00567	151,95263	6	Urban	-32,01167	-32,0116074
23	Edge	-32,00533	151,95202	7	Urban	-32,01176	-32,0116051
24	Edge	-32,00521	151,95229	8	Urban	-32,01192	-32,0116028
9	Park	-32,00665	151,95642				
10	Park	-32,00633	151,95659				
11	Park	-32,0063	151,95638				
12	Park	-32,00579	151,95671				
13	Park	-32,00578	151,95608				
14	Park	-32,00602	151,9559				
15	Park	-32,00531	151,95603				
16	Park	-32,00594	151,9572				

4. Front site Krambach

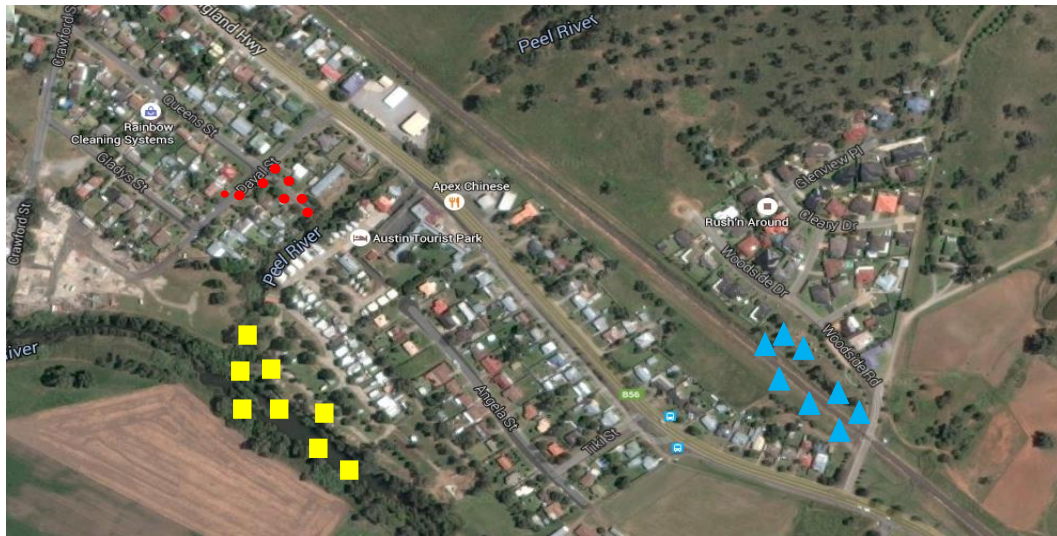


Krambach three habitats

Krambach nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude	Box ID	Habitat	Latitude	Longitude
25	Edge	-32,05295	152,26191	41	Urban	-32,05194	152,260427
26	Edge	-32,05309	152,26162	42	Urban	-32,05165	152,261834
27	Edge	-32,05312	152,26205	43	Urban	-32,05163	152,261509
28	Edge	-32,05244	152,26181	44	Urban	32° 3'5.86"S	152° 15'40.34"E
29	Edge	-32,05291	152,26226	45	Urban	32° 3'5.72"S	152° 15'39.56"E
30	Edge	-32,05292	152,2617	46	Urban	-32,05153	152,260398
31	Edge	-32,05268	152,262229	47	Urban	-32,05145	152,26005
32	Edge	-32,05265	152,26179	48	Urban	32° 3'4.83"S	152° 15'33.96"E
33	Park	-32,05192	152,26335				
34	Park	-32,05182	152,26334				
35	Park	-32,05192	152,263671				
36	Park	-32,05183	152,263545				
37	Park	-32,05203	152,263843				
38	Park	-32,05213	152,263572				
39	Park	-32,05214	152,2625				
40	Park	-32,05212	152,26275				

5. Front Site Tamworth



Tamworth three habitats

Tamworth nest box GPS coordinates			
Box ID	Habitat	Latitude	Longitude
150	Edge	-31,11513	150,9592
151	Edge	-31,11584	150,95918
152	Edge	-31,1157	150,95923
153	Edge	-31,11588	150,95923
154	Edge	-31,11608	150,95921
155	Edge	-31,11626	150,95954
156	Edge	-31,11624	150,96005
157	Edge	-31,11586	150,95959
158	Park	-31,1163	150,96503
159	Park	-31,11612	150,96487
160	Park	-31,11597	150,96466
161	Park	-31,115853	150,96453
162	Park	-31,115729	150,96444
163	Park	-31,115669	150,96429
164	Park	-31,11546	150,96423
165	Park	-31,11554	150,96413
166	Urban	31° 6'51.15"S	150°57'33.71"E
167	Urban	31° 6'52.18"S	150°57'34.73"E
168	Urban	31° 6'51.68"S	150°57'34.82"E
169	Urban	31° 6'51.34"S	150°57'34.45"E
170	Urban	31° 6'50.54"S	150°57'33.84"E
171	Urban	31° 6'50.54"S	150°57'32.76"E
172	Urban	31° 6'52.30"S	150°57'30.83"E
173	Urban	31° 6'49.06"S	150°57'33.75"E



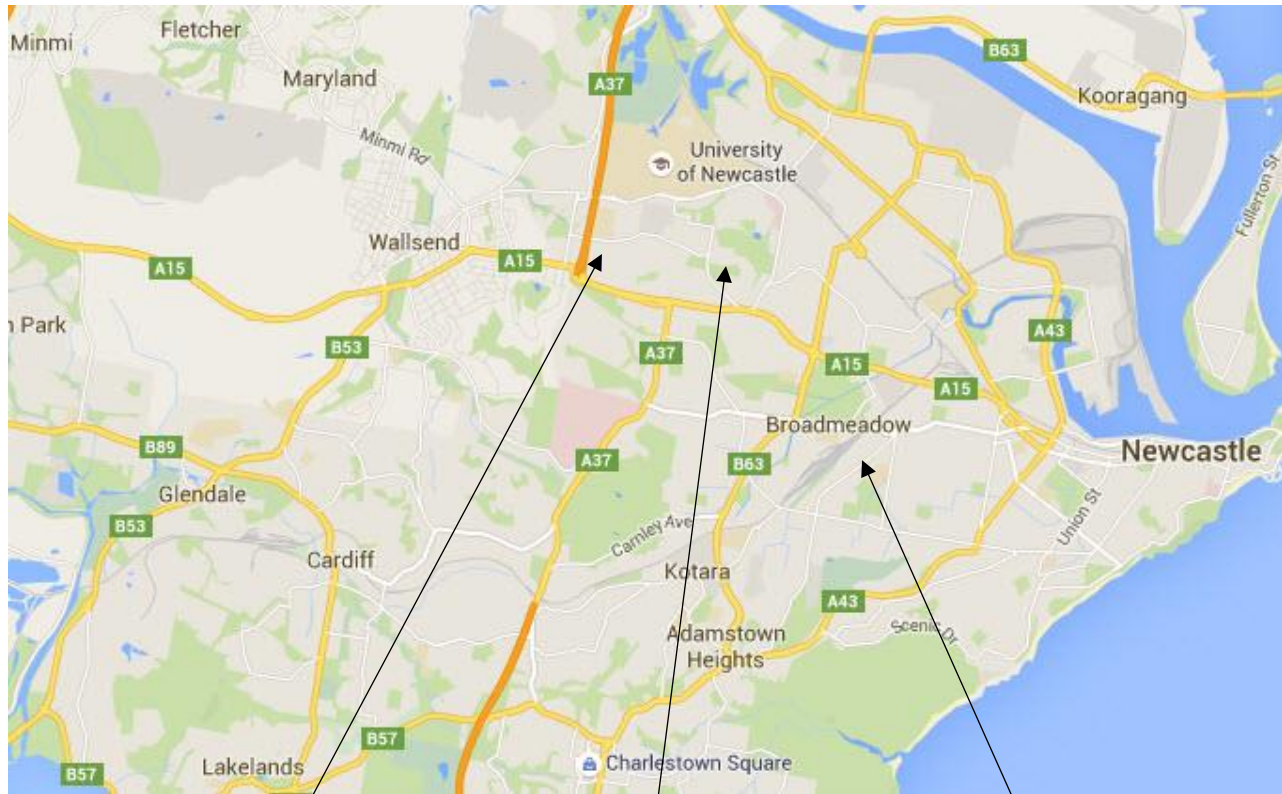
6. Front site Armidale three habitats

Armidale nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude	Box ID	Habitat	Latitude	Longitude
217	Edge	30°30'33.85"S	151°40'30.03"E	209	Urban	-30,515692	151,681115
218	Edge	30°30'33.42"S	151°40'30.79"E	210	Urban	-30,515863	151°40'51.79"E
219	Edge	30°30'33.15"S	151°40'31.64"E	211	Urban	-30,516187	151,680906
220	Edge	30°30'32.59"S	151°40'31.76"E	212	Urban	-30,516344	151,680858
221	Edge	30°30'33.12"S	151°40'33.12"E	213	Urban	-30,516543	151,680783
222	Edge	30°30'33.63"S	151°40'32.64"E	214	Urban	-30,516709	151,680756
223	Edge	30°30'34.02"S	151°40'32.28"E	215	Urban	-30,516926	151,680659
224	Edge	30°30'34.14"S	151°40'31.38"E	216	Urban	-30,517153	151,680557
202	Park	-30,521192	151,684066				
203	Park	-30,521344	151,684098				
204	Park	-30,521501	151,684162				
205	Park	-30,521695	151,684066				
206	Park	-30,521834	151,684361				
207	Park	-30,521682	151,684398				
208	Park	-30,52145	151,684522				

Appendix 2

Three additional sites in Newcastle (30 nest boxes)



Site Hungry Jack
(6 nest boxes)

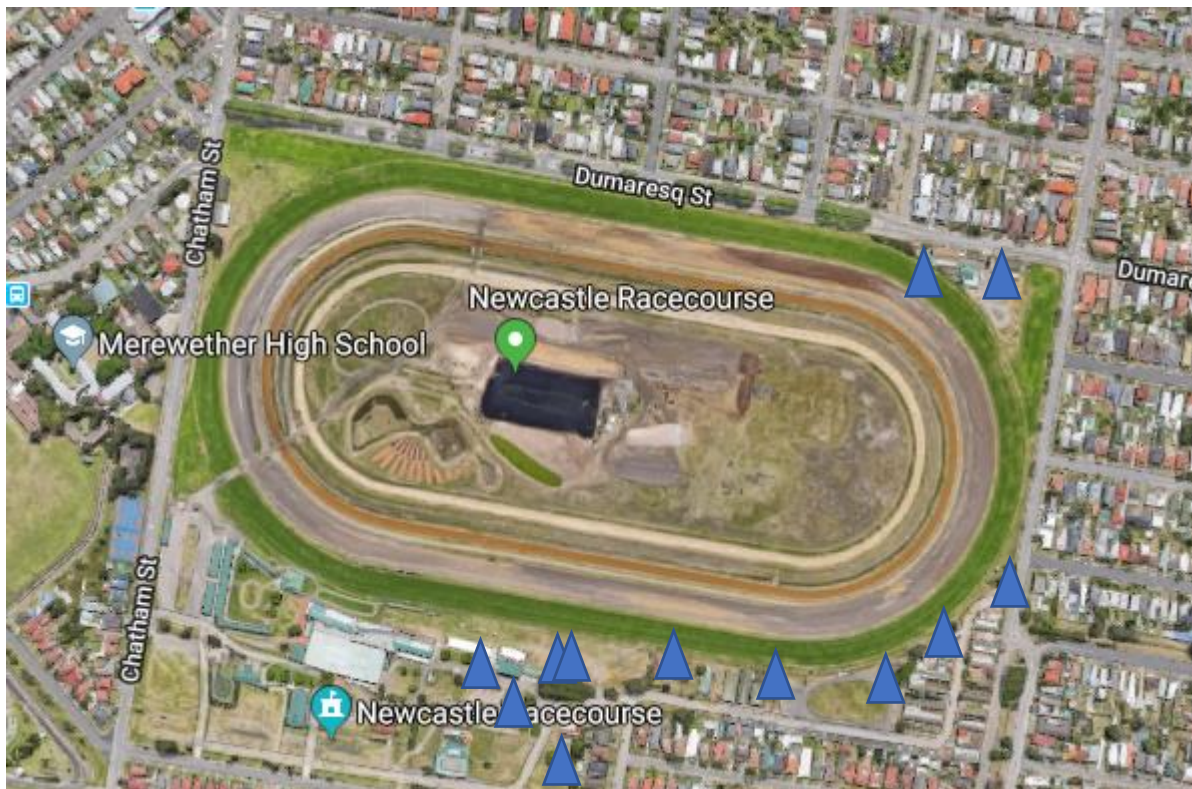
Site Waratah west
Public school
(12 nest boxes)

Site Race Course
Broadmeadow
(12 nest boxes)

1. Site Hungry Jack



2. Race course



Waratah public school



Appendix 3

Nest box locations in Queensland

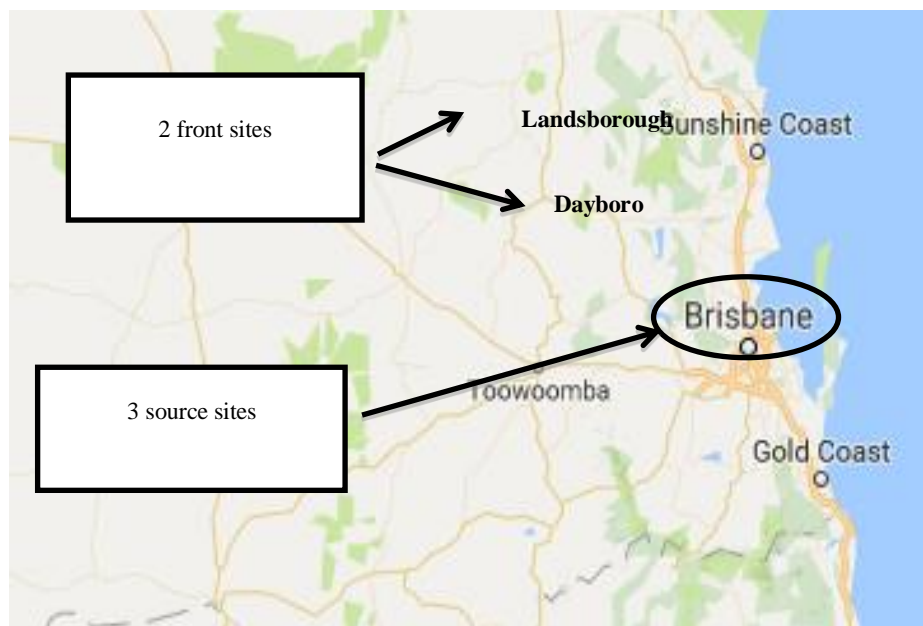
- 3 source sites in Brisbane area (Oxley Creek, Common Norman Park, Gatton)
- 2 front sites (Dayboro, Landsborough)




Each site was divided in three type of habitat: urban, park and edge of the bush.

8 Nest boxes per habitat

24 Nest boxes per site

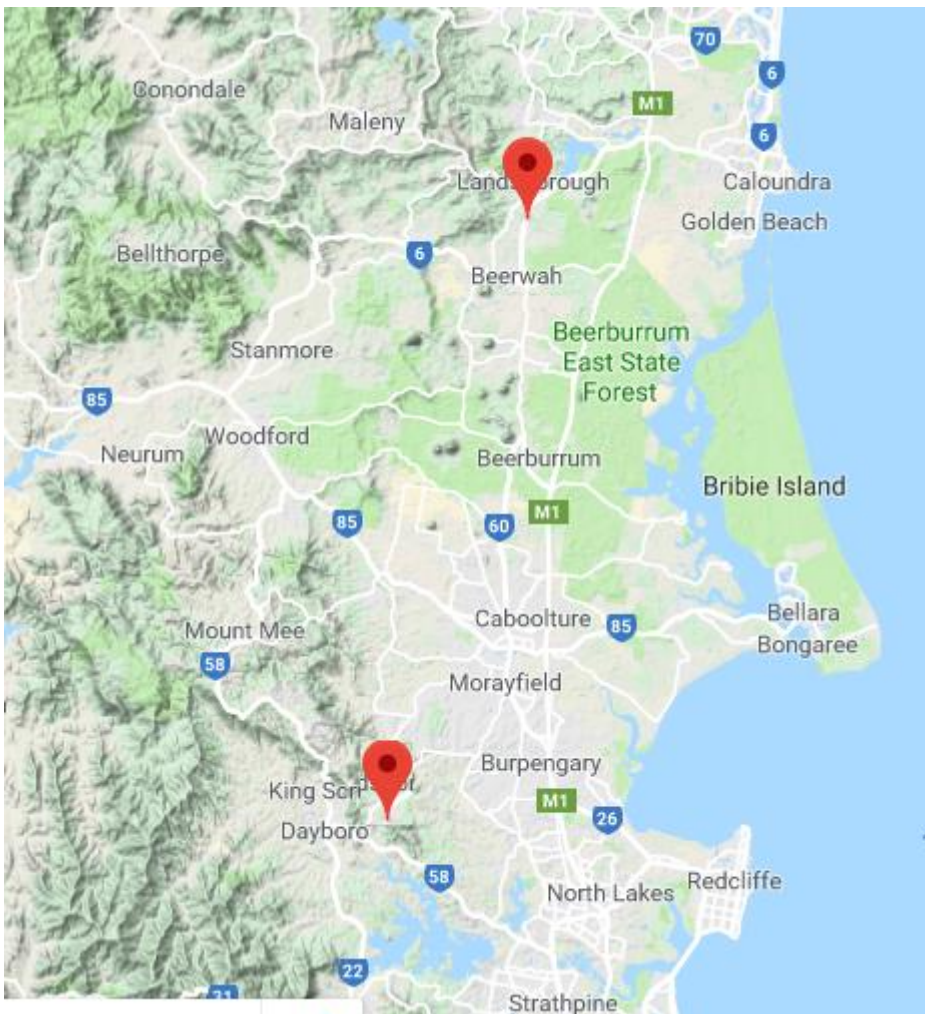
120 Nest boxes in Queensland



	Urban
	Park
	Edge



Source site locations in Brisbane areas



Front site locations

1. Source site Oxley Creek Common



Oxley nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude
1	Park	S27°32'25.9"	E152°59'18.4"
2	Park	S27°32'25.4"	E152°59'18.4"
3	Park	S27°32'23.5"	E152°59'16.7"
4	Park	S27°32'26.7"	E152°59'17.9"
5	Park	S27°32'23.3"	E152°59'15.7"
6	Park	S27°32'22.3"	E152°59'15.9"
7	Park	S27°32'26.5"	E152°59'17.7"
8	Park	S27°32'22.1"	E152°59'15.1"
9	Urban	S27°32'04.6"	E152°59'36.3"
10	Urban	S27°32'04.9"	E152°59'35.9"
11	Urban	S27°32'07.3"	E152°59'32.9"
12	Urban	S27°32'08.7"	E152°59'32.8"
13	Urban	S27°32'08.9"	E152°59'32.7"
14	Urban	S27°32'09.0"	E152°59'33.1"
15	Urban	S27°32'06.4"	E152°59'34.8"
16	Urban	S27°32'08.4"	E152°59'32.3"
17	Edge	S27°32'12.1"	E152°59'26.1"
18	Edge	S27°32'12.4"	E152°59'25.6"
19	Edge	S27°32'12.0"	E152°59'25.0"
20	Edge	S27°32'12.6"	E152°59'24.8"
21	Edge	S27°32'12.9"	E152°59'24.1"
22	Edge	S27°32'12.8"	E152°59'23.9"
23	Edge	S27°32'13.6"	E152°59'24.0"
24	Edge	S27°32'13.9"	E152°59'23.9"

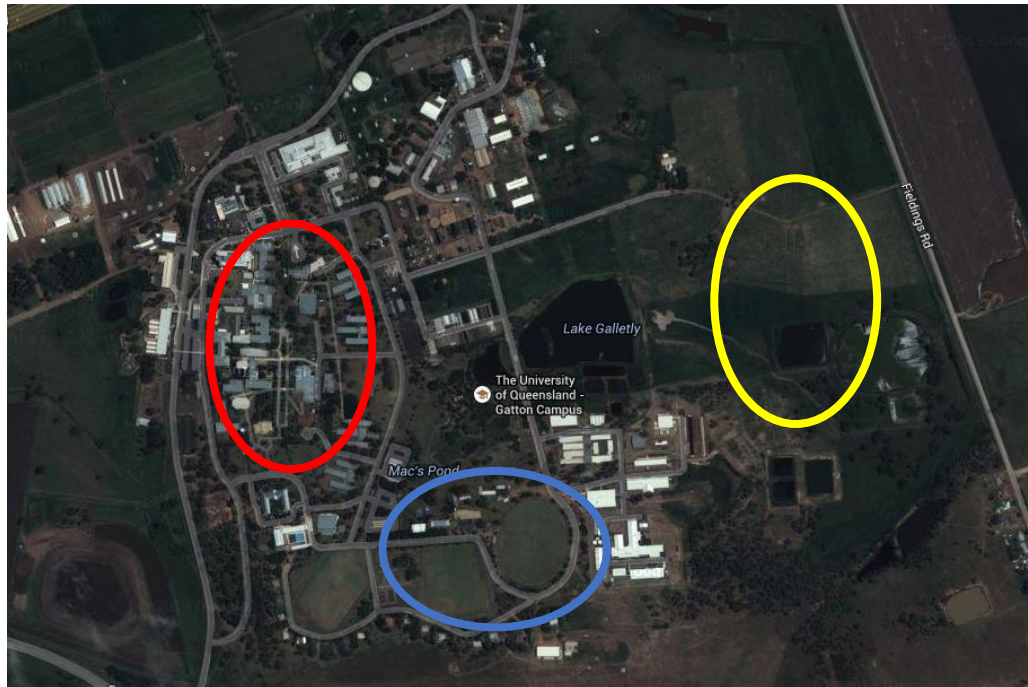
1. Source site Norman Park



Norman Park nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude
26	Edge	S27°29'06.1"	E153°03'07.2"
27	Edge	S27°29'06.6"	E153°03'07.0"
28	Edge	S27°29'12.8"	E153°03'06.0"
29	Edge	S27°29'08.3"	E153°03'05.6"
30	Edge	S27°29'08.8"	E153°03'05.2"
31	Edge	S27°29'14.9"	E153°03'10.5"
32	Edge	S27°29'15.1"	E153°03'07.5"
33	Edge	S27°29'07.8"	E153°03'06.0"
34	Park	S27°29'24.3"	E153°03'04.0"
35	Park	S27°29'24.6"	E153°03'03.3"
36	Park	S27°29'25.2"	E153°03'03.5"
37	Park	S27°29'25.7"	E153°03'02.8"
38	Park	S27°29'23.9"	E153°03'03.7"
39	Park	S27°29'26.2"	E153°03'04.2"
40	Park	S27°29'27.3"	E153°03'05.8"
41	Park	S27°29'27.5"	E153°03'06.2"
42	Urban	S27°29'08.4"	E153°03'11.5"
43	Urban	S27°29'09.2"	E153°03'10.4"
44	Urban	S27°29'09.0"	E153°03'12.1"
45	Urban	S27°29'08.2"	E153°03'12.5"
46	Urban	S27°29'08.7"	E153°03'12.8"
47	Urban	S27°29'08.2"	E153°03'13.5"
48	Urban	S27°29'07.9"	E153°03'13.1"
49	Urban	S27°29'08.8"	E153°03'08.7"

2. Source site Gatton



Gatton nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude
98	Park	S27°33'29.0"	E152°20'22.0"
99	Park	S27°33'32.9"	E152°20'21.4"
100	Park	S27°33'33.2"	E152°20'20.7"
101	Park	S27°33'33.0"	E152°20'19.5"
102	Park	S27°33'30.2"	E152°20'16.1"
103	Park	S27°33'29.5"	E152°20'16.5"
104	Park	S27°33'29.0"	E152°20'16.0"
105	Park	S27°33'29.2"	E152°20'15.4"
106	Urban	S27°33'12.6"	E152°20'01.8"
107	Urban	S27°33'09.7"	E152°20'00.5"
108	Urban	S27°33'07.8"	E152°20'00.3"
109	Urban	S27°33'06.6"	E152°20'02.5"
110	Urban	S27°33'02.4"	E152°20'02.1"
111	Urban	S27°33'03.8"	E152°19'58.2"
112	Urban	S27°33'05.6"	E152°19'52.5"
113	Urban	S27°33'07.4"	E152°19'47.2"
114	Edge	S27°33'18.3"	E152°20'16.8"
115	Edge	S27°33'19.6"	E152°20'18.5"
116	Edge	S27°33'22.1"	E152°20'23.4"
117	Edge	S27°33'23.8"	E152°20'19.9"
118	Edge	S27°33'22.6"	E152°20'20.3"
119	Edge	S27°33'20.9"	E152°20'21.4"
120	Edge	S27°33'19.6"	E152°20'21.6"
121	Edge	S27°33'18.8"	E152°20'21.6"

3. Front site Dayboro



Dayboro nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude
50	Park	S27°11'26.9"	E152°49'05.5"
51	Park	S27°11'25.10"S	E152°49'5.88"
52	Park	S27°11'27.6"	E152°49'08.1"
53	Park	S27°11'28.6"	E152°49'08.5"
54	Park	S27°11'28.3"	E152°49'04.4"
55	Park	S27°11'29.7"	E152°48'59.3"
56	Park	S27°11'30.2"	E152°49'01.3"
57	Park	S27°11'29.0"	E152°49'08.7"
58	Urban	S27°11'38.2"	E152°49'08.7"
59	Urban	S27°11'41.6"	E152°49'09.6"
60	Urban	S27°11'37.9"	E152°49'10.3"
61	Urban	S27°11'40.4"	E152°49'12.1"
62	Urban	S27°11'39.2"	E152°49'13.0"
63	Urban	S27°11'38.7"	E152°49'12.6"
64	Urban	S27°11'39.9"	E152°49'13.2"
65	Urban	S27°11'38.5"	E152°49'12.8"
66	Edge	S27°11'32.0"	E152°48'49.6"
67	Edge	S27°11'32.5"	E152°48'49.4"
68	Edge	S27°11'31.7"	E152°48'49.2"
69	Edge	S27°11'31.9"	E152°48'49.2"
70	Edge	S27°11'31.0"	E152°48'47.4"
71	Edge	S27°11'31.8"	E152°48'47.4"
72	Edge	S27°11'	E152°48'
73	Edge	S27°11'	E152°48'

4. Front site Landsborough



Landsborough nest box GPS coordinates

Box ID	Habitat	Latitude	Longitude
74	Urban	S26°48'12.4"	E152°57'50.4"
75	Urban	S26°48'12.1"	E152°57'51.0"
76	Urban	S26°48'12.5"	E152°57'51.0"
77	Urban	S26°48'12.1"	E152°57'52.2"
78	Urban	S26°48'11.8"	E152°57'52.7"
79	Urban	S26°48'13.5"	E152°57'54.4"
80	Urban	S26°48'13.0"	E152°57'54.8"
81	Urban	S26°48'14.4"	E152°57'51.7"
82	Edge	S26°48'01.7"	E152°58'01.5"
83	Edge	S26°48'01.6"	E152°58'02.1"
84	Edge	S26°48'01.0"	E152°58'02.5"
85	Edge	S26°48'00.5"	E152°58'02.6"
86	Edge	S26°48'00.4"	E152°58'03.2"
87	Edge	S26°47'59.6"	E152°58'05.9"
88	Edge	S26°47'59.1"	E152°58'08.0"
89	Edge	S26°47'58.3"	E152°58'09.9"
90	Park	S26°48'15.6"	E152°57'53.9"
91	Park	S26°48'14.4"	E152°57'54.5"
92	Park	S26°48'14.5"	E152°57'55.0"
93	Park	S26°48'15.9"	E152°57'59.8"
94	Park	S26°48'16.4"	E152°57'59.0"
95	Park	S26°48'15.5"	E152°57'59.8"
96	Park	S26°48'16.6"	E152°57'58.9"
97	Park	S26°48'16.8"	E152°57'58.4"

Appendix 4. Classification of the three most abundant bird species in the three habitats (Edge, Park, Urban) by site in New South Wales and in Queensland. Myna's rank indicates where common myna abundance is situated when bird species are organised from highest to lowest abundance.

State	Study site	Habitat	species 1	species 2	species 3	Myna's rank
NSW	Front 1	Edge	Red wattlebird (<i>Anthochaera carunculata</i>)	Silvereye (<i>Zosterops lateralis</i>)	Australian magpie (<i>Gymnorhina tibicen</i>)	19
NSW	Front 2	Edge	White-headed pigeon (<i>Columba leucomela</i>)	Topknot pigeon (<i>Lopholaimus antarcticus</i>)	Australian raven (<i>Corvus coronoides</i>)	absent
NSW	Front 3	Edge	Australian white ibis (<i>Threskiornis molucca</i>)	Yellow thornbill (<i>Acanthiza nana</i>)	Grey fantail (<i>Rhipidura albiscapa</i>)	18
NSW	Front 4	Edge	Rock dove (<i>Columba livia</i>)	Crested pigeon (<i>Ocyphaps lophotes</i>)	Common myna (<i>Acridotheres tristis</i>)	3
NSW	Front 1	Park	Red wattlebird (<i>Anthochaera carunculata</i>)	Crested pigeon (<i>Ocyphaps lophotes</i>)	Magpie-lark (<i>Grallina cyanoleuca</i>)	5
NSW	Front 2	Park	Rainbow lorikeet (<i>Trichoglossus moluccanus</i>)	White-headed pigeon (<i>Columba leucomela</i>)	Red wattlebird (<i>Anthochaera carunculata</i>)	8
NSW	Front 3	Park	Rainbow lorikeet (<i>Trichoglossus moluccanus</i>)	Australian magpie (<i>Gymnorhina tibicen</i>)	Common myna (<i>Acridotheres tristis</i>)	3
NSW	Front 4	Park	Rainbow lorikeet (<i>Trichoglossus moluccanus</i>)	Australian magpie (<i>Gymnorhina tibicen</i>)	Galah (<i>Eolophus roseicapilla</i>)	12
NSW	Front 1	Urban	House sparrow (<i>Passer domesticus</i>)	Common starling (<i>Sturnus vulgaris</i>)	Magpie-lark (<i>Grallina cyanoleuca</i>)	5
NSW	Front 2	Urban	Common myna (<i>Acridotheres tristis</i>)	Rainbow lorikeet (<i>Trichoglossus moluccanus</i>)	Australian magpie (<i>Gymnorhina tibicen</i>)	1
NSW	Front 3	Urban	Common myna (<i>Acridotheres tristis</i>)	Australian magpie (<i>Gymnorhina tibicen</i>)	Magpie lark (<i>Grallina cyanoleuca</i>)	1
NSW	Front 4	Urban	Common myna (<i>Acridotheres tristis</i>)	Common starling (<i>Sturnus vulgaris</i>)	White-plumed honeyeater (<i>Ptilotula penicillata</i>)	1
NSW	Source 1	Edge	Rainbow lorikeet (<i>Trichoglossus moluccanus</i>)	Noisy miner (<i>Manorina melanocephala</i>)	Welcome swallow (<i>Hirundo neoxena</i>)	6
NSW	Source 2	Edge	Rainbow lorikeet (<i>Trichoglossus moluccanus</i>)	Noisy miner (<i>Manorina melanocephala</i>)	Laughing kookaburra (<i>Dacelo novaeguineae</i>)	absent
NSW	Source 1	Park	Australian magpie (<i>Gymnorhina tibicen</i>)	Magpie lark (<i>Grallina cyanoleuca</i>)	Australian wood duck (<i>Chenonetta jubata</i>)	8

NSW	Source 2	Park	Noisy miner (Manorina melanocephala)	Common starling (Sturnus vulgaris)	Australian magpie (Gymnorhina tibicen)	6
NSW	Source 1	Urban	Common myna (Acridotheres tristis)	Rainbow lorikeet (Trichoglossus moluccanus)	Noisy miner (Manorina melanocephala)	1
NSW	Source 2	Urban	Noisy miner (Manorina melanocephala) 206	Common myna (Acridotheres tristis)	Australian Figbird (Sphecotheres vieillot)	2
QLD	Front 1	Edge	Rainbow lorikeet (Trichoglossus moluccanus)	Silvereye (Zosterops lateralis)	Torresian crow (Corvus orru)	Absent
QLD	Front 2	Edge	Rainbow lorikeet (Trichoglossus moluccanus)	Scaly-breasted lorikeet (Trichoglossus chlorolepidotus)	Magpie lark (Gymnorhina tibicen)	12
QLD	Front 1	Park	Rainbow lorikeet (Trichoglossus moluccanus)	Little corella (Cacatua sanguinea)	Noisy miner (Manorina melanocephala)	15
QLD	Front 2	Park	Rainbow lorikeet (Trichoglossus moluccanus)	Noisy miner (Manorina melanocephala)	Scaly-breasted lorikeet (Trichoglossus chlorolepidotus)	1 seen
QLD	Front 1	Urban	Rainbow lorikeet (Trichoglossus moluccanus)	Australian figbird (Sphecotheres vieillot)	Noisy miner (Manorina melanocephala)	23
QLD	Front 2	Urban	Rainbow lorikeet (Trichoglossus moluccanus)	Noisy miner (Manorina melanocephala)	Scaly-breasted lorikeet (Trichoglossus chlorolepidotus)	1 seen
QLD	Source 1	Edge	Cattle egret (Bubulcus ibis)	Noisy miner (Manorina melanocephala)	Little corella (Cacatua sanguinea)	26
QLD	Source 2	Edge	Noisy miner (Manorina melanocephala)	Rainbow lorikeet (Trichoglossus moluccanus)	Torresian crow (Corvus orru)	16
QLD	Source 3	Edge	Silvereye (Zosterops lateralis)	Red-backed fairywren (Malurus melanocephalus)	Torresian crow (Corvus orru)	38
QLD	Source 1	Park	Rock dove (Columba livia)	Magpie goose (Anseranas semipalmata)	Plumed Whistling duck (Dendrocygna eytoni)	8
QLD	Source 2	Park	Noisy miner (Manorina melanocephala)	Rainbow lorikeet (Trichoglossus moluccanus)	Magpie lark (Grallina cyanoleuca)	7

QLD	Source 3	Park	Rainbow lorikeet (Trichoglossus moluccanus)	Noisy miner (Manorina melanocephala)	Scaly-breasted lorikeet (Trichoglossus chlorolepidotus)	7
QLD	Source 1	Urban	Magpie goose (Anseranas semipalmata)	Little corella (Cacatua sanguinea)	Noisy miner (Manorina melanocephala)	19
QLD	Source 2	Urban	Rainbow lorikeet (Trichoglossus moluccanus)	Noisy miner (Manorina melanocephala)	Torresian crow (Corvus orru)	absent
QLD	Source 3	Urban	Noisy miner (Manorina melanocephala)	Torresian crow (Corvus orru)	Rainbow lorikeet (Trichoglossus moluccanus)	37

To underline when common mynas are present within the most three invasive species on sites, **common myna** was written with bold font.

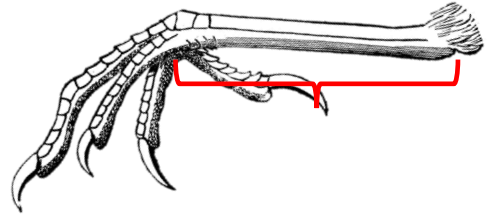
Appendix 5: Bird measurements (Chapter 1)

I undertook four different measurements

1- Tarsus

Start point: the groove within the “ankle”.

End point: where the joint folds.

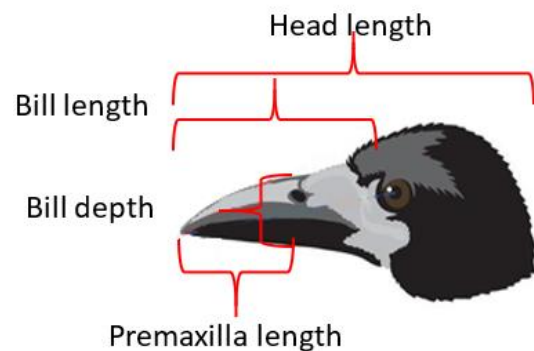


2- Beak

Only Premaxilla

Start point: the front end of the nostril.

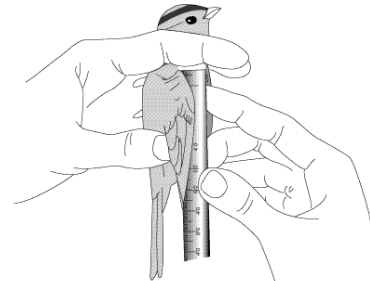
End point: end of bill.



3- Wing

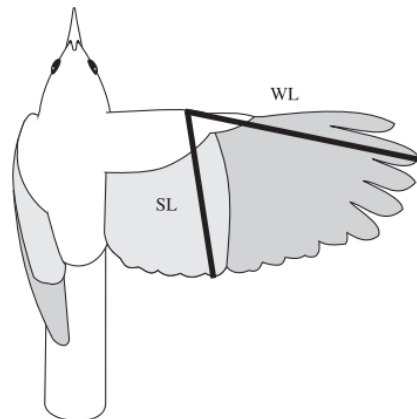
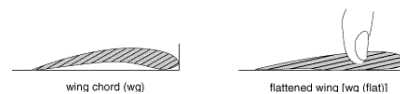
Start point: the bend of the wing

End point: the tip of the longest primary feathers



4- Hand-Wing-Index (HWI)

$$HWI = 100 \times \frac{WL - SL}{WL}$$



From (Claramunt et al. 2012)