2017

Demographic shifts in Noisy Miner (Manorina melanocephala) populations following removal

Jacob A T Vickers

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Abstract
The increasing abundance of Noisy Miners (Manorina melanocephala) represents a large threat to avifaunal assemblages throughout eastern Australia. Their hyper-aggressive colonial social structure has a negative effect on many already threatened small birds, including the critically endangered Regent Honeyeater (Anthochaera Phrygia) and the endangered Swift Parrot (Lathamus discolor). Their increased abundance has consequently been listed as a Key Threatening Process under both state and federal legislation. Culling has been used successfully to reduce the impacts of Noisy Miners and has been suggested as a threat abatement action, however, recolonisation has sometimes been observed. This project aimed to investigate the effects of culling on the demographics of recolonists, to determine the source of recolonists, and thereby improve our understanding of the circumstances when culling may be successful. Additionally, I assessed the efficacy of an ageing technique, and developed a reliable method for sexing Noisy Miners non-destructively. I found that; a) the shape of the alula is not a reliable sexing criterion, b) 90% of Noisy Miners can be correctly assigned a sex using morphometric data, and c) the source of recolonists varied according to the season of the cull, based on the availability of individuals within the landscape. Dispersing immatures comprised the majority of recolonists following the breeding season, whilst matures from neighbouring colonies provided the majority of recolonists beforehand. These findings demonstrate that the time of culling has a significant effect on the type of recolonisation and can be used to assist the development of an effective threat abatement plan.

Degree Type
Thesis

Degree Name
BEnviSc Hons

Department
School of Earth & Environmental Science

Advisor(s)
Kris French

Keywords
Culling, management, birds, threat abatement, age, sex

This thesis is available at Research Online: http://ro.uow.edu.au/thsci/145
Demographic shifts in Noisy Miner (*Manorina melanocephala*) populations following removal

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Supervisors: Prof Kris French and Dr Richard Major

A thesis submitted in partial fulfilment of the requirements for the award of the degree of Bachelor of Environmental Science (Honours)

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October 2017
The information in this thesis is entirely the result of investigations conducted by the author, unless otherwise acknowledged, and has not been submitted in part, or otherwise, for any other degree or qualification.

Signed: ______________________

Date: 24/10/2017
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Acknowledgements

I would like to thank my supervisors, Kris French and Richard Major, who were reliable sources of encouragement and guidance throughout the year. Their positive attitudes and comprehensive feedback made the project fun and manageable. I am indebted to Walter Boles for sharing his ornithological expertise and providing insightful comments on some of the issues that were faced. I would also like to thank my housemates for the good bachie’ banter and builders’ nights, particularly the lovely Anwen Price, who kept me on track and supported me from start to finish. And to my family, thank you for always cheering me on along the way. Lastly, I would like to thank Farzaneh Etezadifar, Kim Maute, Shae Jones, Ebony Zderic, and Sabrina Velasco for preliminary assessment and evaluation of alula shape. I am grateful to Ian and Moira Sirett for their assistance in collection of the Noisy Miner carcasses.

This study used specimens collected from a study assisted by the New South Wales Government through the Environmental Trust. The initial study was authorised by scientific license S101522 under the NSW National Parks and Wildlife Act, with ethics approval granted by the Australian Museum Animal Care and Ethics under the approval number 15/04.
Abstract

The increasing abundance of Noisy Miners (*Manorina melanocephala*) represents a large threat to avifaunal assemblages throughout eastern Australia. Their hyper-aggressive colonial social structure has a negative effect on many already threatened small birds, including the critically endangered Regent Honeyeater (*Anthochaera Phrygia*) and the endangered Swift Parrot (*Lathamus discolor*). Their increased abundance has consequently been listed as a Key Threatening Process under both state and federal legislation. Culling has been used successfully to reduce the impacts of Noisy Miners and has been suggested as a threat abatement action, however, recolonisation has sometimes been observed. This project aimed to investigate the effects of culling on the demographics of recolonists, to determine the source of recolonists, and thereby improve our understanding of the circumstances when culling may be successful. Additionally, I assessed the efficacy of an ageing technique, and developed a reliable method for sexing Noisy Miners non-destructively. I found that; a) the shape of the alula is not a reliable sexing criterion, b) 90% of Noisy Miners can be correctly assigned a sex using morphometric data, and c) the source of recolonists varied according to the season of the cull, based on the availability of individuals within the landscape. Dispersing immatures comprised the majority of recolonists following the breeding season, whilst matures from neighbouring colonies provided the majority of recolonists beforehand. These findings demonstrate that the time of culling has a significant effect on the type of recolonisation and can be used to assist the development of an effective threat abatement plan.
1 - Introduction

The diversity of south-eastern Australian avifauna is currently threatened by multiple converging stressors (Ford et al. 2001; Mac Nally et al. 2009; Ford 2011; Garnett et al. 2014). The most prominent stressor is the extensive loss and fragmentation of native forest habitat throughout Australia, with over 80% of temperate woodlands being cleared since European settlement (Lunt & Bennett 1999; Ford et al. 2001). The impact of such widespread landscape modification is being compounded by climate change (Mac Nally et al. 2009; Bennett et al. 2015b). Increasing mean global temperatures followed by more frequent and intense extreme weather events such as droughts put the survival of many vulnerable species at risk (McAlpine et al. 2009; Bennett et al. 2013; Bennett et al. 2015a). As a result, the large-scale deforestation and landscape change seen in Australia has been the major driving force of bird decline throughout the country (Reid 1999; Garnett & Crowley 2000; Ford et al. 2001; Radford et al. 2005; Szabo et al. 2010).

Landscape change not only affects birds directly through the loss of physical habitat and available resources, but also indirectly through habitat fragmentation and subsequent shifts in interspecific interactions such as predation and competition (Andren 1994; Maron et al. 2011; Bennett et al. 2015a). Changes in the environment can shift interspecific interactions as species respond differently to new environmental pressures, affecting community composition, community dynamics and ecosystem function, having a profound and largely unpredictable effect on the biotic community (Ewers & Didham 2006; Ockinger et al. 2010; Bellard et al. 2012; Bennett et al. 2015a). As extensive landscape change already threatens a wide range of native species it is increasingly important to understand how interspecific interactions are changing in response.

This is especially true when a change in the environment benefits strong interactors, or species that have disproportionately large influences on the assemblage structure (Mac Nally et al. 2012). Whilst not always the case, the over-abundance of a strong interactor or high-impact species can be profoundly detrimental to the health and diversity of the co-occurring community. The proliferation of such a species can prevent other species from accessing vital resources such as food, nesting sites, and shelter due to increased competition. Furthermore, the increased competition can result in drastic changes in community composition as it can create a cascading effect throughout the ecosystem (Howes et al. 2014). Some strong
interactors have hence been termed a “reverse keystone” species (Piper & Catterall 2003) to reflect the negative impact it has on the biotic community. One such species, the Noisy Miner (*Manorina melanocephala*), is a notoriously despotic reverse keystone species and is particularly problematic as it aggressively excludes virtually all smaller heterospecifics from its territories (Piper & Catterall 2003; Maron *et al.* 2011; Mac Nally *et al.* 2012).

1.1 - The Noisy Miner

The Noisy Miner is a moderately large honeyeater (c. 60g) endemic to eastern Australia with a native range of over 3000km from tropical Queensland to temperate Tasmania. Unlike many honeyeaters which track flowering patterns, they are sedentary and live in large high-density colonies consisting of up to several hundred birds, covering up to 40 hectares (Dow 1977; Higgins *et al.* 2001). By adopting flexible foraging behaviour and a varied diet of insects, nectar, fruit, and psyllid lerp, they have access to the abundant year-round food needed to maintain high-density colonies with energetically expensive territorial defence (Dow 1977; Higgins *et al.* 2001). Exploiting multiple food sources and foraging substrates eliminates the need to roam in search of seasonal nectar sources like many other nectarivorous birds (Saunders *et al.* 2003; Ashley *et al.* 2009; Maron 2009). The constraint of dependency on local food sources is partly overcome by the control of food and space through the aggressive mobbing of potential competitors, resulting in the exclusion of almost all smaller bird species (< 63g) (Mac Nally *et al.* 2012).

The Noisy Miner is hyper-aggressive to both conspecifics and heterospecifics, not only defending its territory from predators and competitors, but all intruders, including species with negligible ecological overlap (Higgins *et al.* 2001). Expelling small birds from open forests takes less energy and is far more cost-effective than chasing birds through dense foliage. It is for this reason that Noisy Miners are thought to prefer open woodlands, particularly isolated patches of open eucalypt forest with sparse understorey (Higgins *et al.* 2001; Oldland *et al.* 2009). Due to a strong preference for woodlands adjacent to grassy clearings, Miners generally reside 150-300m from woodland edges but can go further depending on forest density (Piper & Catterall 2003; Clarke *et al.* 2007). Edge habitats in open eucalypt woodlands are often dominated by these “aggressive edge specialists” (Major *et al.* 2001), as they generally
comprise a simple understorey structure that facilitates the detection and removal of territorial intruders (Loyn 1987; Grey et al. 1998; Mac Nally et al. 2012).

European agricultural practices such as deforestation, grazing and increased fire frequencies have modified much of eastern Australia’s rural landscape, inadvertently establishing vast areas of habitat optimal for Noisy Miner colonisation (Hobbs & Hopkins 1990; Oldland et al. 2009). As a result, there has been a substantial decline in rural woodland birds from the combined effects of habitat loss and interference competition within remaining woodland patches dominated by Noisy Miners (MacNally 1983, 1999; Major et al. 2001). A threshold density for a significant negative correlation between bird diversity and Noisy Miner density has been identified (Thomson et al. 2015), with densities as little as 0.64 Miners per hectare having a negative impact on bird assemblages.

Small patches of remnant forest support higher densities of Miners than in large patches, and can often become fully occupied by a colony because it is more manageable to defend smaller areas (Clarke & Oldland 2007). Although a Noisy Miner colony generally cannot dominate an entire large contiguous remnant forest, they seek out and occupy its most productive areas, gaining exclusive control of rich soils that support the greatest density of invertebrates and nectar-producing plants (Recher et al. 1996; Oldland et al. 2009). The most productive areas of a landscape are generally selected and cleared for agriculture, leaving adjacent woodlands with the rich soils sought by Miners. Additionally, nutrients are trapped by woodland edges and corners, adding to the benefits such habitats already provide to Noisy Miners (Murcia 1995). Much of the remaining uncleared land in central NSW is set aside for Travelling Stock Routes (TSR), which comprise mainly edge habitat. TSR’s are thin corridors of public reserves used for travelling or grazing stock, and they general abut agricultural properties. These corridors of remnant woodland are characteristic of the ideal Noisy Miner habitat as they have vast edge habitat and minimal understorey due to heavy grazing. However, Miners are also common in other human-modified landscapes.

The presence of Noisy Miners in urban environments has been well-documented as they have recently become ubiquitous in Sydney, Melbourne, Brisbane, and many towns throughout eastern Australia (Catterall et al. 2002; Parsons et al. 2006). The heightened disturbance and background noise from human and vehicular traffic has less impact on Noisy Miners than found on many other birds (Lowry et al. 2011, 2012). In fact, the species have been termed “urban adapters” as they flourish in such an environment, displaying significantly greater disturbance.
tolerance and intensity of aggression than their rural counterparts (Lowry et al. 2011; Rudder 2016). Food availability in urban environments can often be complemented by novel and opportunistic items such as rubbish, food scraps, and even sugar sachets (Taylor et al. 2013; Delgado-V & Correa-H 2015). Other urban food sources are relatively consistent for nectarivorous birds due to the selection of plants with long and complementary flowering periods, including cultivated banksias, callistemons, hybrid grevilleas, and eucalypts, which suit the foraging strategy of the sedentary Noisy Miner (Griffioen & Clarke 2002; Low 2002; French et al. 2005; Ashley et al. 2009). As an abundance of food is usually dominated by larger aggressive honeyeaters, most aggressive interactions between birds in urban environments are initiated by Noisy Miners, which usually involves competition over food (Ford & Paton 1976; Taylor et al. 2013). This behaviour has resulted in a significant decrease in the abundance and diversity of small urban-dwelling birds where Miners are present (Parsons et al. 2006; Taylor et al. 2013). The ability of Noisy Miners to opportunistically use a broad range of native and exotic plants coupled with their large size and hyper-aggressive domination of resources has led to their highly successful colonisation of urban and rural environments.

1.1.1 - Social structure

The Noisy Miner is an obligate cooperative breeder with a highly complex and gregarious colonial social structure (Higgins et al. 2001). Individuals are never found in simple pairs; instead they reside year-round in discrete colonies, which can reach up to several hundred birds in open dry sclerophyll woodlands (Dow 1979b). Although the colonies occupy discrete areas, the precise boundaries of a colony are difficult to identify as aggregations can cover vast areas and consist of many sub-units, known as ‘coterries’ (Dow 1979a; Põldmaa et al. 1995; Higgins et al. 2001). Coterries are the most stable social units within the colony and usually contain no more than 25 individuals (Dow 1979a). Individuals spend most of their time in small discrete areas within the colony known as their activity space (Dow & Whitmore 1990). Although female activity spaces do not overlap, the activity space of males overlap widely, causing them to associate more often and form the stable coterie group, which usually contains in its area one or more females (Dow 1979a). However, females occasionally nest outside the area occupied by a coterie, and as such the stability of a coterie can be compromised when males frequently leave to attend nests (Dow 1979b). Males visiting from other coteries elicit more
intense and sustained aggression than found between members of the same coterie (Higgins et al. 2001).

Due to the gregarious nature of Noisy Miners, most activities occur communally in temporarily formed groups termed ‘coalitions’. Coalitions are transitory flocks that form sporadically with membership changing frequently over space and time, as it consists of birds whose activity spaces overlap at the location and time of formation (Dow & Whitmore 1990). Coalitions tend to comprise members of the same coterie as activities often take place within their overlapping activity spaces. Such groups are generally small consisting of 5-8 individuals and form during activities such as preening, feeding, bathing, roosting, and anting (Higgins et al. 2001). The largest coalitions form during mobbing events, where up to 40 birds originating from various coteries cooperatively mob birds, mammals and reptiles, expelling them from the colony’s territory (Dow 1977; Clarke 1984; Higgins et al. 2001).

Throughout a colony, females defend their activity space from other females, resulting in the uniform distribution of females, whereas males do not defend their activity spaces, and move relatively freely throughout the colony (Dow 1979a). Although female boundaries are usually upheld through mutual avoidance rather than aggression, a female bird will aggressively chase any female intruders from its area (Dow 1978). Consequently, young female birds that are unable to establish their own activity space are often forced to disperse from the colony. For displaced females to survive, they must either find free space within another colony, survive by themselves, or found their own colony. However, this is often unsuccessful as most other colonies will also be female-saturated, individuals are rarely seen living by themselves, and founding a colony requires breeding pairs and favourable environmental conditions. Therefore, the high rates of female dispersal result in high mortality rates, which is consistent with the male-biased adult sex ratio found within a colony (Dow 1977, 1978; Arnold et al. 2001).

Noisy Miners breed year-round, but most breeding occurs during the more productive months of spring (Higgins et al. 2001). Females build nests without the help of males, taking up to six days to complete. A clutch of two to four eggs is generally laid anywhere between two and 10 days after nest completion, with a further 16 days to complete the incubation period (Dow 1978). Females are solely responsible for incubation and spend most of their time at the nest. Males are later important in the development of the young as they become attracted to vocalising nestlings, frequently visiting nests to deliver food, remove faecal sacs and perform other nesting behaviours (Põldmaa et al. 1995). Helpers are almost always males, with some
broods provisioned by up to 22 helpers with feeding rates reaching over 85 provisions per hour (Dow 1978; Arnold et al. 2001). Nestlings are thought to fledge after 14 days (Arnold et al. 2005), after which they continue to be fed for up to 35 days out of the nest (Dow 1978). After 11 weeks, juveniles that remain near nests or continue begging for food are attacked by mature males, including paternal males that contributed most to the provisioning of the juvenile (Dow 1978).

A female nesting within a coterie is assisted mostly by males affiliated with that coterie, whereas females nesting in areas of the colony that are not occupied by coteries are assisted by males from adjacent coteries (Dow 1979b). Noisy Miners are monogamous and never raise chicks without helpers, and whilst it is unclear what benefits helpers receive, a high degree of relatedness may exist within coteries between helper and breeder, suggesting extended family relationships may play a key role in communal breeding (Põldmaa et al. 1995; McDonald et al. 2016).

The role of feeding the young is the most easily quantified act of helping a breeding pair, however cooperative breeding also includes tasks such as territory and predator defence (Brown 1987). Most helpers both provision and defend nests, with paternity almost always being assigned to the male that provisions the nest at the highest rate. Arnold et al. (2005) found that birds who contributed greatest to provisioning often contributed little to defence, and vice versa, suggesting a division of labour within the cooperative breeding system. The presence of any heterospecifics near a nest, whether a known predator or a novel intruder, provokes an almost immediate aggressive mobbing response (Arnold et al. 2001; Arnold et al. 2005). In most cases, more birds act to defend the brood by assisting in mobbing coalitions, than by provisioning the chicks (Arnold et al. 2005). The role of a helper may be determined by physiological mechanisms, such as behavioural syndromes resulting in birds more inclined to either provision or mob (Sih et al. 2004).

Helpers that frequently mob intruders in proximity to a nest may not necessarily have any relation to the brood, creating an uncertainty surrounding the benefit they receive and hence their motivation to exert energy and increase their own risk of predation. However, it has been argued that the benefits do not rely solely on the survival of the brood, but also on gaining social status (Zahavi & Zahavi 1999), experience (Heinsohn 1991), reciprocated assistance (Kokko et al. 2001), and possibly, due to the highly complex social structure, not being evicted from the group (Johnstone & Cant 1999).
The survival of immature males provides indirect benefits to the parents as they are rewarded with philopatric helpers that increase their future reproductive output (Põldmaa 1996). Due to this social structure, it is likely that a sex-biased preference for males exists (McDonald et al. 2010). Although primary sex ratios are even, the first egg to hatch in a clutch is significantly more likely to be male than female, however it is unclear whether this is due to an adaptive ability of the female controlling sex allocation or simply that males develop faster in the egg (Arnold et al. 2001). Sex-biased hatching results in advanced males which are likely to fledge first with a greater survivorship than subsequent eggs, and reciprocate aid to their parents and coterie. Thus male-biased sex ratios are expected in colonies through the combined effects of higher nestling survival of males and female-biased dispersal.

The most commonly cited explanation for biased sex-ratios in cooperatively breeding birds is the helper repayment hypothesis (Emlen et al. 1986), which suggests a sex-bias for the philopatric sex as they are the most cost-effective. Males are often the philopatric sex, and male-biased sex ratios have been observed in many species of cooperatively breeding birds (Brown 1987; Koenig & Walters 1999; Clarke, MF et al. 2002; Doutrelant et al. 2004).

Adult Noisy Miner populations, like those of its congeners, have invariably been found to be male-biased, which is consistent with the helper repayment hypothesis as males are the only philopatric sex. There are no reports of female-biased or even sex ratios in adults, even though the sex ratio of nestlings has consistently been found to be at parity (Arnold et al. 2001; Higgins et al. 2001; Barati 2017). Previous studies have found the magnitude of male-bias to range between 2.1:1 and 4.7:1 (Dow & Whitmore 1990; Arnold et al. 2001; Barati 2017). A male-bias of 2.1-2.5:1 was observed in the northern tablelands of NSW at three different colonies (Barati 2017), slightly less than the 2.2-3.3:1 male-bias reported by Dow (1978) and Arnold et al. (2001) in south-eastern Queensland. In comparison, Clarke et al. (1990) and Clarke et al. (2002) found the closely related bell Miner (Manorina melanophrys) had a male-bias sex ratio of 1.7-1.8:1 in populations in Victoria, although primary sex ratios are male-biased in this species (Clarke & Heathcote 1990; Clarke, MF et al. 2002). Additionally, Ewen et al. (2001) found a male-bias sex ratio of 1.2-2.6:1 in the endangered black-eared Miner (Manorina melanotis) in populations in South Australia (Murray Mallee), yet a female-bias primary sex ratio was observed (Ewen et al. 2001).
1.1.2 - Key threatening process

The Noisy Miner is particularly proficient at adapting to human-disturbed ecosystems, as habitat modification, such as land clearing, is often to the benefit of their highly aggressive and cooperative social structure. This has led to their increased abundance throughout open and fragmented woodlands of eastern Australia, often resulting in populations so numerous that they comprise over 50% of all birds present (Loyn 1987; Clarke & Oldland 2007; Maron 2007; Mac Nally et al. 2012). Birds most affected by the Noisy Miner’s aggression are smaller species (< 63g: Mac Nally et al. 2012) such as small honeyeaters, flycatchers, foliage gleaners and aerial insectivores (Clarke 1984; Grey et al. 1997; Eyre et al. 2009). Larger birds are targeted to a lesser extent, while some birds, such as the Grey Butcherbird (Cracticus torquatus), can share intermittent associations with the Noisy Miner during antipredator responses (Fulton 2008; Maron 2009). A direct response to the proliferation of the hyper-aggressive species has been a noticeable decline in many small woodland bird species throughout urban and rural landscapes, often resulting in Noisy Miners being the only small to medium sized species remaining (Dow 1977; Grey et al. 1997; Grey et al. 1998; Piper & Catterall 2003; Clarke & Oldland 2007; Howes & Maron 2009). Size dependent exclusion of birds has led to additional indirect pathways in which small birds are adversely affected, as sites dominated by the species are generally only left with large-bodied and often aggressive nectarivores, granivores, and carnivores which further deter smaller bird species (Bayly & Blumstein 2001; Maron et al. 2013). Additionally, the expulsion of small leaf-gleaning birds releases predatory pressures on leaf-feeding invertebrates, causing significant damage to tree health through increased leaf loss and dieback (Loyn et al. 1983; Wardell-Johnson et al. 2005). The defoliation and canopy dieback caused by dense colonies may also assist in maintaining the open habitat structure beneficial to Miners (Grey et al. 1998; Kutt et al. 2012). Furthermore, the pollination and hence gene flow of trees and shrubs between fragmented woodlands may be interrupted as highly mobile pollinators are excluded and replaced with sedentary Miner colonies (Maron et al. 2013). In this way, Noisy Miners contribute to habitat degradation which if left unmanaged may affect the long-term health of woodlands and the species dependent upon them (Paton 2000; Southerton et al. 2004).

The aggressive exclusion of small birds by the Noisy Miner has adversely affected multiple species of birds listed under the Threatened Species Conservation Act 1995 (NSW), including the critically endangered Regent Honeyeater (Anthochaera Phrygia) and the endangered Swift
Parrot (*Lathamus discolor*) (Higgins *et al.* 2001; Saunders & Heinsohn 2008). Consequently, the NSW Scientific Committee made a final determination to list the “aggressive exclusion of birds from woodland and forest habitat by abundant Noisy Miners *Manorina melanopephala*” as a key threatening process under the *Threatened Species Conservation Act 1995* (NSW) as it: a) adversely affects threatened species, populations, or ecological communities, and b) causes species, populations or ecological communities that are not threatened to become threatened. The Noisy Miner is currently listed as a key threatening process both by the state (*Threatened Species Conservation Act 1995* (NSW), listed 27 September 2013) and federally, following advice to the Minister of the Environment from the Threatened Species Scientific Committee (*Environment Protection and Biodiversity Conservation Act 1999* (Cth), listed 7 April 2014).

Listed key threatening processes are matters of state or national environmental significance that provide official recognition of the threat to national biodiversity. This is followed by the consideration of a threat abatement plan, which if determined to be a feasible, effective, and efficient plan will be used to establish a national framework through which a response can be guided, coordinated and enforced. In this case, it was decided that a national threat abatement plan for the hyper-abundant Noisy Miner was not feasible, however, state-wide programs can be implemented if a strategy is found to contribute significantly to the abatement of their impact.

1.2 - Threat abatement plan

There are a range of strategies available to mitigate the influence of Noisy Miners on bird assemblages. Most available strategies are based on the strong correlation between open eucalypt woodlands and high Noisy Miner density. These strategies generally focus on reducing edges, corners and protrusions, and increasing the structural complexity of woodlands, particularly the understorey vegetation, to create habitat less susceptible to Noisy Miner domination (Hastings & Beattie 2006; Clarke *et al.* 2007; Taylor *et al.* 2008). This is done by increasing revegetation efforts, decreasing grazing and adopting a less frequent fire regime, essentially reversing the effects of European agricultural practices. However, the vast loss of woodland habitat cannot simply be reversed (Maron *et al.* 2011), and certainly not at a national scale. It is important to avoid inappropriate revegetation efforts that inadvertently
create additional Noisy Miner habitat, such as planting fast growing eucalypts in small or linear patches, or in vegetation communities in which eucalypts are rare (e.g. Buloke remnants), resulting in the colonisation of Miners where they were not previously present (Watson et al. 2000). The presence of as few as five eucalypts per hectare, especially species that produce copious nectar such as White Box (Eucalyptus albens) and Blue Gum (Eucalyptus leucoxylon), is a strong predictor of Noisy Miner occupancy (Lunt & Bennett 1999; Oldland et al. 2009). Whilst habitat modification strategies may be effective at the scale of single properties, there has been little success to date (Hastings & Beattie 2006; Debus 2008). The current habitat modification practices of revegetation and habitat rehabilitation are time consuming and have an inherent time lag in the provision of habitat resources for different species, as habitat resources change as vegetation matures (Vesk & Mac Nally 2006; Vesk et al. 2008; Thomson et al. 2009). Due to the constraints on time and the current potential impacts on other fauna, habitat modification is unlikely to be a feasible threat abatement action at a national scale.

Direct culling of Noisy Miners has been attempted in a limited number of small-scale trial studies (Grey et al. 1997; Debus 2008), with promising results for threat abatement. Grey et al. (1997, 1998) found that the removal of Noisy Miners from small (< 10 ha) woodland remnant patches was followed by an influx of small insectivorous birds and a substantial increase in bird abundance and diversity, with some sites remaining free of Noisy Miners for years following removal. Similarly, Debus (2008) found a dramatic increase in the species richness of small insectivorous birds after Noisy Miners were culled from multiple properties. Following the promising results of these studies, culling has been proposed as the most cost-effective and humane method of mitigating Noisy Miner impacts (Clarke & Grey 2010). Furthermore, the return of small, mobile insectivorous birds is associated with improved tree health, as they control the abundance of leaf-feeding insects that contribute to rural dieback (Loyn 1987; Catterall et al. 1991; MacDonald & Kirkpatrick 2003). The implications of these findings suggest removal of Noisy Miners from larger woodland habitats may be an effective threat abatement plan with long-term benefits for biodiversity in affected areas (Grey 2008), particularly when accompanied with appropriate habitat rehabilitation efforts.

Following Grey’s work (1997, 1998), a study is being undertaken to determine whether culling is feasible as a threat abatement action when extrapolated to larger sites (10-80 ha) (Davitt 2016). In addition to sites in the New England Tablelands, the study is occurring across 12 sites in the Western Slopes Bioregion, an area dominated by open woodlands of grey box (Eucalyptus microcarpa) and white cypress pine (Callitris glaucophylla). These sites are the
focus of the present study. From the 12 sites, six were randomly chosen for a Noisy Miner removal treatment, with control treatments assigned to the remaining six sites. Each site was located on a section of Travelling Stock Route which comprise corridors of open eucalypt woodland adjacent to agricultural land that is actively farmed for sheep and grain production. All sites were selected using the criteria that they supported Noisy Miner colonies as determined from surveys of Miners using song playback.

The study involved three removals in August 2015, September 2015, and April 2016, during which Noisy Miners were culled using a 12-guage shotgun. The geographic location of Miners was recorded with an accuracy of 20 m, and their carcasses collected, individually labelled and retained in frozen storage. Bird surveys were carried out before the first removal began, and following each removal thereafter, to collect information on all species present as well as their abundance. Although only a small decrease in Noisy Miner abundance was observed following the removals (Davitt 2016), there was a significant increase in the abundance and diversity of small insectivorous birds. The relative proportion of Noisy Miners in the population fell from 38% to 29% over the duration of the study, changing the composition of the avifaunal assemblage and likely further reducing interspecific aggression. However, Noisy Miners later returned and re-established colonies following removal, suggesting culling efforts may not be feasible as a threat abatement action at larger scales.

The different outcomes from this study and the experiments of Grey and Davitt are perplexing (Grey et al. 1997; Grey et al. 1998; Davitt 2016), and before concluding that culling has no place in threat abatement, it is important to gain a better understanding of why the sites culled by Davitt (2016) were recolonised so quickly. A key issue in developing this understanding is determining the source of the recolonising birds. Specifically, were they 1) recolonists comprised of birds that fled the sites while culling was occurring, 2) new individuals moving in from other parts of the landscape, or 3) whole colonies that shifted from other sites into the vacated space? These three alternatives are likely to have different demographic signatures related to the species’ social structure. In particular, the higher occurrence of female dispersal due to limited space and the resultant male-biased sex ratio within colonies, is likely to be reflected in the sex ratio of recolonists.

Due to the high occurrence of female dispersal, most of the individuals wandering throughout the landscape would likely be immature and female. If these wandering individuals were to drive the rapid recolonisation of culled sites, we could expect to find a high proportion of
females and immatures within newly established colonies. Alternatively, a newly established colony with a similar sex ratio and age structure to the original colony may be representative of a whole neighbouring colony shifting into the vacated space, or recolonists that fled during culling. Colonies with demographic characteristics differing from the normal state may not express the same behaviours nor have equivalent impacts on small bird species as colonies in equilibrium. Measuring these characteristics within newly re-established colonies may assist us in understanding why small bird species were still able to establish within sites that were recolonised by Noisy Miners following removal (Davitt 2016).

1.3 - Determining the sex and age of Noisy Miners

Sexing individuals is often necessary when undertaking ecological studies, particularly when the species of interest has a social structure resulting in skewed sex ratios. Assigning sex to individuals of the family Meliphagidae can be difficult without intrusive or molecular methods as honeyeaters typically have sexually monomorphic plumages. However, it is often the case in apparently monochromatic species that one sex is larger than the other (Collins & Paton 1989). Noisy Miners are sexually monomorphic with no differences in plumage between sexes (Higgins et al. 2001). They are however sexually dimorphic in size, with males being the larger sex, although this is not visually apparent and can only be determined by measuring individuals (Rogers et al. 1986). There is currently no reliable method to sex the species without the use of invasive or molecular techniques, or the opportunistic sighting of individuals performing gender-specific tasks, such as nest building, sexual displays, incubating, or making the territorial ‘pew’ vocalisation (Dow 1975; Dow 1978; Holt et al. 2017). Many studies have successfully used multivariate statistical methods, such as discriminant function analysis and logistic regression, to predict the sex of individuals based on morphometric data (Pohar et al. 2004; Gill & Vonhof 2006; Jakubas & Jakubas 2011).

Multivariate statistical methods have been used successfully to develop sexing equations for all three of the Noisy Miner’s congeners. The equations developed were able to predict the sex of individuals with high classification rates for each of the three sexually dimorphic congeners; Bell Miners (M. melanophrys), Yellow-throated Miners (M. flavigula), and Black-eared Miners (M. melanotis) (Clarke & Heathcote 1988; Clarke, RH et al. 2002). Following these studies, it
is likely that a similar approach would yield an accurate and reliable equation for sexing Noisy Miners in the field.

The ability to readily age animals is of huge benefit to ecology as it can assist in studies dependant on the ability to manage and monitor a population’s demographic structure. The Noisy Miner displays no clear indicator of age, as found in the colour of the closely related bell Miner’s (*M. melanophrys*) eye-patch (Clarke & Heathcote 1988). According to Higgins (2001), juveniles, although similar in appearance, are distinguishable from immature and adult individuals by softer plumage with minor variations in colour. Immatures displaying partial post-juvenile (first pre-basic) moult can be distinguished from adults by retained juvenile coverts or alula, in at least some cases, but the consistency of this characteristic across the cohort is unknown. Once post-juvenile moult is complete then first year birds are identical to adults, and as it is not known at what age juvenile (first pre-basic) moult begins, the assessment of plumage for ageing is often redundant. An alternative method commonly used by museum researchers and bird-banders is determining the degree of skull pneumatisation, which is a particularly useful tool when plumage characteristics have become identical to that of adults. However, most literature on skull pneumatisation focusses on birds that are endemic to the northern-hemisphere, as they are subjected to strong seasonal cycles, making them much more predictable and consistent in timing. While it is not yet known at what age the Noisy Miner skull becomes completely pneumatized, pneumatisation is a good candidate character for assessing the state of maturity, as song-birds generally complete pneumatisation at four to eight months of age (Serventy *et al.* 1967). An additional character that might be useful for ageing Noisy Miners is the shape of the alula feathers, which Matthew (1999) suggested can provide information on the age of an individual. Although, again, such a marker can only prove useful for ageing birds within a specific age range, after which they can only be assigned ‘adult’.

1.4 - Research questions

The process of developing a feasible and effective threat abatement plan would benefit from a greater understanding of how Noisy Miners respond to culling. Investigating any changes in demographic characteristics between pre-cull and post-cull populations may assist in understanding how recolonisation occurs after such action. Further understanding provides the
foundation on which appropriate guidelines can be created, paving the way towards the successful management and mitigation of the key threatening process.

This study seeks to assess any change between the demography of birds present before and after removal, to evaluate alternative hypotheses for the rapid recolonisation of woodland patches from which Noisy Miners have been removed. In order to achieve this it is necessary to evaluate potential ageing and sexing criteria for Noisy Miners. Accordingly, this study has three specific aims:

1) to evaluate current ageing techniques and determine suitable ageing criteria for Noisy Miners,

2) to establish criteria for sexing Noisy Miners by developing a morphometric model based on birds of known sex, determined by dissection, and

3) to compare the age and sex structure of resident and recolonising Noisy Miner populations.

Each of the above aims were addressed in separate chapters as they were developed as standalone manuscripts for submission to a journal. Consequently, there is some repetition between each chapter’s introduction and methods as it was necessary to repeat some relevant background information. The results will be used to explore how large-scale removals might impact the demography of Noisy Miner colonies and the implications for future management of the Noisy Miner key threatening process.
2 - The use of alula shape for ageing Noisy Miners

This chapter is currently in review by Corella as:

The use of alula shape for ageing Noisy Miners (*Manorina melanocephala*) – a critical evaluation


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2.1 - Introduction

Ecological studies focussing on understanding the population processes of birds often require knowledge about the age of individuals (Sun 2001). As such, the ability to age birds has been the backbone for many studies on species conservation, invasive species management, survivorship, demography and the impacts of environmental stressors on avian populations (Brook *et al.* 2003; Sun *et al.* 2011; King *et al.* 2013; Shao *et al.* 2015; Diller *et al.* 2016). Many methods exist for the age determination of passerines, including assessment of an individual’s plumage, degree of skull pneumatization, colour of bill and bare-skin patches, and behaviour (Miller 1946; Norris 1961; Counsilman & King 1977; Gargallo & Clarabuch 1995; Higgins *et al.* 2001; Jenni & Winkler 2011). Plumage is a popular ageing characteristic as it is easy and quick, if persistent plumage differences are present. However, in species that undergo a complete post-juvenile moult into an immature that has adult-like first plumage, ageing using plumage is constrained beyond a simple assessment of adult versus juvenile. Such species are particularly difficult to age, and require alternative ageing techniques.

The Noisy Miner (*Manorina melanocephala*), like many other passerines, fledges in a distinct juvenile plumage (Higgins *et al.* 2001). Sometime after fledging, the first immature plumage
is acquired through either a partial or complete post-juvenile moult, which may be dependent upon fitness, diet, and environmental conditions (Jenni & Winkler 2011; Minias & Iciek 2013; Kiat & Izhaki 2016). Complete post-juvenile moult results in plumage indistinguishable from that of adults, whilst a partial post-juvenile moult is adult-like, but distinguishable by retained juvenile inner primaries, secondaries, and/or alula (Dow 1973; Higgins et al. 2001). When about one-year old, most Noisy Miners undergo the second pre-basic moult from immature to adult plumage (Higgins et al. 2001). As the Noisy Miner displays no alternative clear indicator of age, such as the colour of the eye-patch of the closely related Bell Miner (M. melanophrys) (Clarke & Heathcote 1988), the development of alternative ageing techniques for field identification is necessary.

Differences in the shape of the longest feather of the alula between juveniles and adults has been suggested as an alternative method for identifying adult-like first immatures: juveniles are suggested to have a broad alula with a rounded tip, whereas birds with a narrow, pointed alula are suggested to be adults (Matthew 1999). Matthew (1999) proposed this was true for 43 species of Meliphagidae, including the Noisy Miner, and found it “probable that these birds replace the juvenile alula in the second pre-basic moult, when about one-year old”. The study examined museum skins of both immature and adult birds to assess differences in the shape of the alula. However, there has been no critical evaluation of the reliability of the alula shape as an ageing characteristic for Noisy Miners that are not aged as museum specimens.

Whilst undertaking a study involving the dissection of Noisy Miners, the opportunity arose to record both external characteristics and internal anatomy to investigate ageing criteria. The aim of this study was to determine whether the shape of the longest feather of the alula is a reliable characteristic for age determination of live Noisy Miners.

2.2 - Methods

We analysed Noisy Miner carcasses collected from a study involving the experimental removal of this species from remnant eucalypt woodlands (Davitt 2016). The removals took place in August and September 2015 and April 2016 near the town of Fifield (-32.808 S, 147.463 E) within the Western Slopes Bioregion of south-eastern Australia. Carcasses were frozen until this study commenced in February 2017.
The longest feather of the right alula of each Miner was examined and classed as either “round” or “sharp” following the diagram presented in Matthew (1999); however, this classification was problematic as the alula’s shape was often ambiguous (Fig. 2.1). Following this, dissections were used to determine the age of birds by assessing the degree of skull pneumatisation, the presence of a bursa of Fabricius (bursa, hereafter), and the state of the oviduct in females. Skull pneumatisation was assessed by peeling back the skin, following an incision in the crown, and classified as either “minimal”, “partial”, or “complete”. The bursa was classed as “present” or “absent”, and oviducts were examined and classed as “straight” or “convoluted”. A convoluted oviduct indicates that the bird has previously laid an egg (Christians & Williams 1999; Vézina & Williams 2003).

![Figure 2.1. Examples of the longest feather of the right alula taken from different individuals. A) Sharp alula taken from an immature; B) Sharp alula taken from a mature; C) Round alula taken from an immature; D) Round alula taken from a mature; E) Ambiguous alula classed as round; F) Ambiguous alula classed as sharp.](image)

Noisy Miners are capable of breeding after their first year (Dow 1978), and the observed age-of-first-breeding of the closely-related Bell Miner is 8.3 months for males and 9.7 months for
females (Clarke & Heathcote 1990). Therefore, Noisy Miners with convoluted oviducts were assumed to be at least 8 months of age. As it is not known at what age the Noisy Miner’s skull becomes completely pneumatised, or at what age the bursa involutes, an exact age could not be determined from these characteristics. They are good candidates for assessing the state of maturity, however, as songbirds generally complete pneumatisation by 4-8 months of age (Serventy et al. 1967), and the bursa – an immunosuppressive organ in young birds – generally involutes after 2-6 months, depending on the species (Glick 1983; Ciriaco 2003). Therefore, all individuals with a bursa were considered first immatures, as were all Miners with minimal or partial skull pneumatisation (Dow 1978). For the purpose of this study, all other birds were classified as “mature”, recognising that this category will be over-represented.

After a training phase to develop consistent categorisation and measurement, which involved dissection and analysis of 271 specimens in consultation with experienced museum ornithologists, data were collected on 476 individual Miners by a single researcher (JV). Data were analysed and significance was tested using contingency tables and associated Chi-square and Fisher’s Exact tests. Statistical analyses were performed using JMP Pro software version 11 and IBM SPSS software version 21.

2.3 - Results

Of the 476 birds examined, 101 (21.2%) showed minimal pneumatisation (clear skull), 46 (9.7%) showed partial pneumatisation, and 316 (66.4%) showed complete pneumatisation, with 13 (2.7%) unidentifiable (owing to excessive damage) (Fig. 2.2). The probability of an individual having a bursa significantly reduced with skull pneumatisation ($\chi^2 = 289.8$, N=463, p < 0.001), as it was present in 74.3%, 15.2%, and 0%, of birds with minimal, partial, and complete pneumatisation, respectively. Using the criterion that mature birds had both involute bursas and full skull pneumatisation, 316 Miners were classed as mature with the remaining 147 Miners classed as immature.
All birds were anatomically sexed, and the state of the oviducts in 186 females was identified. There was a significant difference in the proportion of females with convoluted oviducts between birds of different age, based on skull pneumatisation ($\chi^2 = 73.1$, N=186, p < 0.001). No birds (N=48) showing minimal pneumatisation had convoluted oviducts, 50% (N=14) of individuals showing partial pneumatisation had convoluted oviducts, and 72.6% (N=124) of individuals showing complete pneumatisation had convoluted oviducts (Fig. 2.3). No birds that showed any sign of a bursa were observed to have convoluted oviducts.
Using the criterion that mature birds had both involute bursas and fully pneumatised skulls, the probability of an immature Noisy Miner having a round alula (Fig. 2.4) was significantly greater than for an adult (Fisher’s Exact, \( p < 0.0001 \), \( N=460 \); Fig. 2.4). Round alulas were found on 40.7\% (\( N=145 \)) of all immature Miners, and 20.3\% (\( N=315 \)) of all mature Miners (Fig. 2.4).

There was a significant seasonal difference in the proportion of birds with round alulas (Fisher’s Exact, \( p = 0.013 \), \( N=460 \); Fig. 2.5). Immature birds sampled in spring 2015 showed a significantly greater proportion of round alulas than matures (Fisher's Exact, \( p < 0.0001 \), \( N=283 \); Fig. 2.5), with 66.7\% (\( N=27 \)) of immature Miners and 18.0\% (\( N=163 \)) of mature Miners showing round alulas. However, birds sampled in autumn 2016 showed no significant difference in the proportion of alulas between age classes (Fisher’s Exact, \( p = 0.615 \), \( N=177 \); Fig. 2.5), with 34.8\% (\( N=118 \)) of immatures showing round alulas, compared with 30.5\% (\( N=59 \)) of matures. Additionally, the probability of an individual having a round alula did not differ between sexes (Fisher’s Exact, \( p = 0.667 \), \( N=447 \)).
2.4 - Discussion

This study demonstrated that age determination in Noisy Miners is complex using both anatomical and field characters. The presence of a bursa of Fabricius and incomplete skull pneumatisation were clearly associated with younger birds, but neither character was completely reliable. Some birds with negligible pneumatisation had involute bursas, and some birds with large bursas exhibited partial pneumatisation. However, as the frequency of an individual having a bursa dropped from birds with minimal to partial pneumatisation, and was not found at all in Miners with complete pneumatisation, the bursa is probably involuting well before the skull becomes completely pneumatised. Additionally, as Noisy Miners with convoluted oviducts are assumed to be at least 8 months old, and half the birds showing partial pneumatisation had convoluted oviducts, it appears that complete pneumatisation may occur after eight months of age. Alternatively, some females could breed at an age younger than eight months. Without known-age birds or reliable anatomical ageing characters, evaluating the reliability of alula shape as a field character for ageing Miners proved to be challenging. Furthermore, many alula feathers were shaped ambiguously, and their assignment as “round” or “sharp” was difficult and subjective.
There was a significant association between age and alula shape, with immatures having twice the incidence of round alulas as matures. However, a significant proportion of mature individuals were also found to have round alulas, demonstrating that this character is not diagnostic. Furthermore, the majority of immatures in the autumn sample – most of whom were born in the previous spring (Morris et al. 1981) – displayed sharp alulas, suggesting round alulas can be lost well before six months old. Although it is likely that a small portion of birds were incorrectly classified as mature based on our anatomical definition, this discrepancy alone cannot explain the large number of mature Noisy Miners with round alulas. There was an unexpected seasonal effect on the proportion of individuals with round alulas, as immature Miners were far more likely than matures to exhibit round alulas in spring, compared with autumn, when the proportion of round alulas did not differ between ages. However, the small sample size of immatures in spring should be noted. The seasonal variation in alula frequency could not be explained as there was no intersex variation in alula frequency, and although there were more immatures than matures in autumn, they were likely too young to have completed pneumatisation and inflate misclassification rates. Samples of known-age birds are necessary to resolve this uncertainty.

It is conceivable that the removal treatment itself may have had an unforeseen effect on the development of individuals, which may have influenced the frequency distribution of alula shape in the autumn sample. Specifically, only one third of immature birds had round alulas in autumn, much less than in the initial spring removal. Birds sampled in autumn were collected from the same sites as the spring sample, so they were likely to be recolonists, rather than an independent sample of birds (Davitt 2016). Reduced intraspecific competition and the consequent increase in food availability may influence the proportion of first immatures that undergo complete post-juvenile moult (Minias & Iciek 2013; Kiat & Izhaki 2016), resulting in a lower proportion of immatures with round alulas. It could also be the case that an extensive post-juvenile moult is beneficial for immatures entering habitat free of well-established Noisy Miner colonies, as it reduces their juvenile characteristics, increasing their dominance status and their ability to compete in the following winter (Gosler 1994). Given the complexity of Noisy Miner social structure (Dow 1979; Higgins et al. 2001) it is possible that disruption of colonies may be a driver of unusual development patterns in addition to the more usual factors of season, competition, and food availability.

Regardless of the cause, alula feather shape is evidently an inconsistent ageing character for Noisy Miners. The alula was suggested (Matthew 1999) as a good ageing characteristic to use...
when an immature has moulted its juvenile primaries, secondaries and coverts, and is identical to adults, and whilst it is true that an immature Miner is more likely to have a round alula than a mature, the use of this as an ageing characteristic for either a single individual or a population is not an appropriate method and should only be used as a rough estimate, if at all.

The unexpected variability in anatomical characters in this study resulted in uncertain estimates of the reliability of alula shape as a field character. Given this variability it appears that reliability of alula shape as an ageing character can only be determined by an investigation of known-age birds which will entail tracking them from fledging. Such an approach is feasible, given that long-term colour-banding studies are in train (Barati et al. 2016), but will be labour intensive if conclusive sample sizes are to be obtained. However, even without knowledge of the magnitude of error in alula-based age determination, it is clear that this is not a reliable character. Further studies are also needed to determine the rate of pneumatisation for the Noisy Miner and the age at which the bursa of Fabricius begins involution. With this information, a more accurate assessment of the alula could be achieved and would allow future studies to explore the effects of intraspecific interactions, food availability and season on the shape of the alula feathers.
3 - Sexing the Noisy Miner using morphometrics

3.1 - Introduction

The ability to correctly sex birds is often required in ecological studies that include life-history traits, ecological interactions, social frameworks and/or population demographics. The methods used by researchers to identify the sex of individual birds, and the degree of difficulty in doing so, can vary greatly depending on the amount of sexual dimorphism exhibited by the species. Sexing is particularly difficult for many sexually monochromatic bird species, as they often show no readily distinguishable differences between sexes. Consequently, studies requiring the assignment of sex to individuals of such species are often forced to rely on costly and time-consuming methods, such as molecular sexing from a blood, tissue, or feather sample (Griffiths et al. 1998). However, removing feathers for DNA extraction can be an unreliable method that can have negative impacts on an individual’s fitness and chances of survival (McDonald & Griffith 2012). Alternative methods such as laparotomies – a lateral incision in the posterior ribs to view the gonads – can be used to sex individuals, but is invasive and, in rare circumstances, can lead to death through internal bleeding (Berthold 1969). It is desirable, therefore, to identify methods of sexing that minimise financial and time costs for researchers as well as impacts on the subject’s health.

Although sex may not be readily identifiable in many monochromatic species, it is often the case that one sex, usually the male in passerines, is larger than the other (Andersson 1994). Consequently, morphological measurements of sexually dimorphic species can be an effective tool for sexing birds in the hand, and have been used extensively for the sexing of many monochromatic species that are seemingly indistinguishable visually (Dechaume-Monchamart et al. 2011).

Like many cooperatively breeding honeyeaters, the Noisy Miner (Manorina melanocephala) is sexually monochromatic and cannot be easily sexed without the opportunistic sighting of gender-specific traits such as brood patches, or behaviours such as nest building, incubation, or certain displays (Dow 1975; Dow 1978; Pöldmaa et al. 1995; Arnold et al. 2001). Although most cooperative breeders are similar in size between sexes, Noisy Miners are sexually dimorphic in size, with larger males (Dunn et al. 2001; Higgins et al. 2001). Whilst this is not visually apparent, it can be determined through the measurement of individuals, although
considerable overlap exists between sexes (Dow 1975; Rogers et al. 1986; Higgins et al. 2001). Many previous studies have used univariate and multivariate statistics to develop equations on which live birds can be readily sexed through one or more easily attainable field measurements (Green & Theobald 1989; Woehler et al. 1989; Hallgrimsson et al. 2008). Most commonly used models for sex prediction include a binary linear regression (BLR) (Jeffrey et al. 1993; Gill & Vonhof 2006), or discriminant function analysis (DFA) (O'Dwyer et al. 2006; Berkunsky & Reboreda 2009) as both models can produce similarly efficient equations (Pohar et al. 2004). DFA’s have been used previously to successfully predict sex for three sexually dimorphic and closely related species of the same genus; Bell Miners (M. melanophrys), Yellow-throated Miners (M. flavigula), and Black-eared Miners (M. melanotis) (Clarke & Heathcote 1988; Clarke, RH et al. 2002). Following these studies, it is likely that a similar approach would yield an accurate and reliable equation for the effective sexing of Noisy Miners.

A univariate discriminant function has been applied to the measurements of wings of Noisy Miners (Plant 1983, as reported in Higgins (2001)) and produced the following equation: C = 0.123 x Wing length (mm) – 16.067, where birds with C < 0 were assigned male, and female if C > 0. However, this equation could only correctly sex 59% of birds. As the Noisy Miner has a large overlap between sexes, the sample size used in the study (N=79; 45 males and 34 females) may not have been adequate to quantify the species’ sexual dimorphism. Furthermore, the study was based on museum skins, which can differ from live birds by a shrinkage of 3-4 mm in the dried skins (Fullagar & Disney 1981). Consequently, it remains the case that no efficient field sexing technique exists for the Noisy Miner.

The aim of this study was to further quantify sexual dimorphism in the Noisy Miner through the application of discriminant function analysis on the morphometric measurements of individuals whose sex had been confirmed via dissection, and ultimately develop a reliable and widely applicable sexing equation for use in the field.
3.2 - Methods

Study site

As part of a wider experiment investigating the restoration of woodland bird communities by culling of Noisy Miner populations (Davitt 2016), individuals were removed from six sites in travelling stock routes, within 100km of each other. The removals took place in August and September 2015 and April 2016 near the town of Fifield (-32.808 S, 147.463 E) within the Western Slopes Bioregion of NSW. All carcasses were collected and frozen until this study commenced in February 2017.

Data collection

Morphological measurements were taken by six recorders from a total of 707 individuals (Table 3.1) from all sites and removals (Table 3.2), and sex was determined by dissection. Of the 707 Noisy Miners, 476 were adults (281 males and 197 females), and 227 were immature (111 males and 116 females). Up to six morphometric measurements were recorded from all individuals using standard bird banding protocols (Rogers et al. 1986): body weight; wing length with chord flattened and straightened, measured with a stopped ruler from the carpal joint to the tip of the longest primary; tarsus, measured from the intertarsal joint to the distal end of the tarsometatarsus; culmen, from bill tip to feathering; total head length, from base of skull to tip of bill; and tail, from the base to the tip of the longest tail feather. Measurements of wing and tarsus were taken from the individual’s right-hand side unless the wing or leg was damaged, in which case the left appendage was used. Wing and tail were measured with a ruler (± 1mm), while tarsus, culmen, and head to bill were measured with vernier calipers (± 0.01mm). These measurements were selected as they are considered to be easily measured in the field, and have been successfully used in similar studies on sexual dimorphism in monochromatic species (Iko et al. 2004; Shephard et al. 2004; Jakubas & Jakubas 2011; Ura et al. 2016).

Although a large proportion of birds were recorded by a single recorder (JV), multiple recorders contributed to the dataset (Table 3.1), and inter-observer variation was therefore a potential issue as it often occurs in such measurements (Gosler et al. 1998; Pitzer et al. 2008). Inter-observer variation was assessed using Student’s t-tests to compare the mean value for each
variable measured by JV with the mean value measured by all other recorders. The impact of multiple observers was found to be negligible as only culmen length differed significantly between recorders ($t = 6.41, p < 0.0001$; Appendix A.1). As a result, and in keeping with the objective of developing a general sexing criterion, discriminant function analyses were conducted using the combined data from all recorders. This approach provides a more conservative equation that incorporates inter-observer variation and provides a more widely applicable equation for workers in the field (Clarke et al. 2003; Jakubas & Jakubas 2011).

Table 3.1. The number of individual Noisy Miners measured by each of six recorders (#1-#6). Data from 65% of individuals were collected by a single recorder (JV).

<table>
<thead>
<tr>
<th>Recorder</th>
<th>#1 (JV)</th>
<th>#2</th>
<th>#3</th>
<th>#4</th>
<th>#5</th>
<th>#6</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Individuals</td>
<td>460</td>
<td>58</td>
<td>56</td>
<td>52</td>
<td>43</td>
<td>38</td>
<td>707</td>
</tr>
</tbody>
</table>

Table 3.2. Number of Noisy Miners processed from each of six sites collected in three sessions of removal.

<table>
<thead>
<tr>
<th>Site</th>
<th>C08</th>
<th>C32</th>
<th>C35</th>
<th>C42</th>
<th>C45</th>
<th>C52</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug-15</td>
<td>55</td>
<td>53</td>
<td>48</td>
<td>49</td>
<td>20</td>
<td>43</td>
<td>268</td>
</tr>
<tr>
<td>Sep-15</td>
<td>40</td>
<td>24</td>
<td>40</td>
<td>32</td>
<td>17</td>
<td>17</td>
<td>170</td>
</tr>
<tr>
<td>Apr-16</td>
<td>64</td>
<td>48</td>
<td>48</td>
<td>47</td>
<td>32</td>
<td>30</td>
<td>269</td>
</tr>
<tr>
<td>Total</td>
<td>159</td>
<td>125</td>
<td>136</td>
<td>128</td>
<td>69</td>
<td>90</td>
<td>707</td>
</tr>
</tbody>
</table>

Univariate characterisation of morphometric variation

Student’s $t$-tests were used to test multiple morphological characteristics for significant differences between male and female Noisy Miners. Bonferroni correction was used on all $t$-tests to compensate for the increased likelihood of Type I errors that are caused by running multiple tests on an individual. Additionally, to determine whether separate sexing equations were necessary for immature and mature individuals, $t$-tests were used to test for significant morphometric differences between the age groups. Inter-age variation was tested separately for each sex because sex ratios differed between samples of immature and mature individuals, with matures having a significantly higher proportion of males ($\chi^2_1 = 6.096, N=705, p = 0.014$). Distinguishing age in this species is difficult (Higgins et al. 2001), particularly in the field. If feasible, it would therefore be beneficial to develop a sexing equation derived from the
combined measurements of immature and mature individuals, as it would not require the bird to be aged prior to sexing.

*Identification of the best parameters for discrimination between sexes*

An initial step-wise discriminant analysis was performed after all morphometric measurements were taken from 407 birds to determine which parameters best predicted sex (Appendix A.2). Weight was excluded from the analysis as it is not a measure of structural size (Piersma & Davidson 1992) and can fluctuate seasonally. Rao’s V was used as the selection criteria for the step-wise procedure (Rao 1952), with a threshold value taken from a table of critical chi square values. The five variables used allowed four degrees of freedom and the change in V for a new variable to be entered was statistically significant at \( p < 0.05 \) (Klecka 1980). Following this criterion, new variables were entered when the change in Rao’s V > 9.49 and F > 3.84 (\( p = 0.05 \)), and variables removed when F < 2.71 (\( p = 0.10 \)). We used a jackknife (leave-one-out) cross-validation technique, where each case is classified by the function calculated from all other cases. The analysis was re-run three times with randomised subsamples to check the validity of the results, ensuring correct identification of the best predictors (Manly 2004).

*Discriminant function analysis*

A single recorder (JV) then continued to collect data from the remaining 300 Noisy Miner carcasses, measuring only the parameters identified in the initial step-wise discriminant analysis as the best predictors of sex. DFA’s were performed using only these parameters, incorporating all 707 recorded individuals. We used a jackknife cross-validation technique, followed by a 50:50 holdout analysis (sample-splitting), to reduce bias and avoid overly optimistic discriminant rates (Ryder 1978; Tabachnick & Fidell 2006; Hair *et al.* 2010; Dechaume-Moncharmont *et al.* 2011). Due to unequal sample sizes between sexes, prior probabilities were based on group sizes, and results were chance-corrected using Cohen’s kappa (Titus *et al.* 1984). All statistical analyses were performed using IBM SPSS software V21.

Two functions were developed in this way, providing an equation with the best discrimination rate, and an equation which incorporates only the single morphometric measurement that is most efficient for use in the field. The applicability of the DFA was tested across space, time,
and observers by developing functions using; individuals from a single site to predict the sex of individuals from all other sites, individuals from the first removal to predict the sex of individuals from all other removals, and; individuals measured by a single recorder to predict the sex of individuals measured by all other recorders, and vice versa.

Some morphological measurements could not be taken from all carcasses due to damage from shooting, and accordingly the DFA only included those cases with all relevant measurements. All data were tested for the assumptions of a discriminant analysis: linearity, normality, multicollinearity and homogeneity of variance-covariance matrices. Discriminant analyses are highly sensitive to multivariate outliers, which were expected due to the large sample size (Manly 2004; Osborne & Overbay 2004). Two extreme outliers were identified using Mahalanobis distance, and were removed from analysis as they were found likely to be erroneous (Tabachnick & Fidell 2006).

3.3 - Results

Univariate characterisation of morphometric variation

Noisy Miner males of mixed ages were found to have a significantly larger body weight, wing length, head-bill length, tail length, culmen length, and tarsus length when compared with females of mixed ages (Table 3.3). The percentage sexual dimorphism of morphological characteristics varied between 3.0% (tarsus length) and 11.3% (weight), with wing length having the largest sexual dimorphism (6.3%) of all the parameters used in the discriminant analysis (Table 3.3). Percentage dimorphism was calculated as:

\[
\% \text{ dimorphism} = \frac{\text{mean}_{\text{male}} - \text{mean}_{\text{female}}}{\text{mean}_{\text{female}}} \times 100
\]

Due to the combined effect of significant sexual dimorphism (Table 3.3) and significantly different sex ratios between immature and mature birds, differences between age groups were assessed independently for each sex to avoid Type I errors. Males displayed no significant morphometric differences between ages in all parameters except wing length, which was
significantly larger in mature males than immature males \((t = 4.32, p < 0.0001, \text{Table 3.4})\).

Females showed no significant differences between ages in all parameters except tail length, which was found to be significantly larger in immature females than mature females \((t = -2.68, p = 0.008, \text{Table 3.4})\).

**Table 3.3.** Morphometric measurements and percentage dimorphism of male and female Noisy Miners. All individuals were sexed via dissection, and equal variances are assumed. Means are shown with ± 1SD, and \(p\) values are considered significant if \(p < 0.0083\) after Bonferroni correction. *represents significance of Student’s \(t\)-test results.

<table>
<thead>
<tr>
<th>Character</th>
<th>Males</th>
<th>Females</th>
<th>t-test</th>
<th>% dimorphism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Mean</td>
<td>df</td>
<td>t ratio</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>63.0 ± 4.2</td>
<td>56.6 ± 4.7</td>
<td>686</td>
<td>19.10</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>137.9 ± 4.2</td>
<td>129.7 ± 4.1</td>
<td>669</td>
<td>25.05</td>
</tr>
<tr>
<td>Head length (mm)</td>
<td>48.3 ± 1.1</td>
<td>46.2 ± 1.1</td>
<td>669</td>
<td>24.09</td>
</tr>
<tr>
<td>Tail (mm)</td>
<td>122.4 ± 5.5</td>
<td>117.8 ± 6.0</td>
<td>395</td>
<td>7.99</td>
</tr>
<tr>
<td>Culmen (mm)</td>
<td>18.6 ± 1.4</td>
<td>17.7 ± 1.1</td>
<td>384</td>
<td>6.61</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>31.2 ± 1.4</td>
<td>30.3 ± 1.3</td>
<td>391</td>
<td>6.00</td>
</tr>
</tbody>
</table>

**Table 3.4.** Morphometric measurements and percentage dimorphism of immature and mature Noisy Miners. The comparison is separated by sex because of variation in sex ratios between samples of immature and mature individuals. All individuals were sexed via dissection, and equal variances are assumed. Means are shown with ± 1SD, and \(p\) values are significant if \(p < 0.0083\) after Bonferroni correction. *represents significance of Student’s \(t\)-test results.

<table>
<thead>
<tr>
<th>Character</th>
<th>Immature</th>
<th>Mature</th>
<th>t-test</th>
<th>% dimorphism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Mean</td>
<td>df</td>
<td>t ratio</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>63.8 ± 4.5</td>
<td>62.7 ± 4.0</td>
<td>384</td>
<td>-2.21</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>136.4 ± 4.5</td>
<td>138.4 ± 4.0</td>
<td>379</td>
<td>4.31</td>
</tr>
<tr>
<td>Total head length (mm)</td>
<td>48.2 ± 1.2</td>
<td>48.3 ± 1.1</td>
<td>375</td>
<td>0.54</td>
</tr>
<tr>
<td>Tail (mm)</td>
<td>123.5 ± 5.8</td>
<td>122.0 ± 5.3</td>
<td>232</td>
<td>-1.89</td>
</tr>
<tr>
<td>Culmen (mm)</td>
<td>18.5 ± 1.6</td>
<td>18.8 ± 1.4</td>
<td>225</td>
<td>1.24</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>31.3 ± 1.4</td>
<td>31.2 ± 1.4</td>
<td>230</td>
<td>-0.48</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Character</th>
<th>Immature</th>
<th>Mature</th>
<th>t-test</th>
<th>% dimorphism</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Mean</td>
<td>df</td>
<td>t ratio</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>56.6 ± 4.7</td>
<td>56.6 ± 4.6</td>
<td>300</td>
<td>0.02</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>129.5 ± 4.2</td>
<td>129.9 ± 4.0</td>
<td>288</td>
<td>0.81</td>
</tr>
<tr>
<td>Total head length (mm)</td>
<td>46.1 ± 1.1</td>
<td>46.3 ± 1.1</td>
<td>292</td>
<td>1.44</td>
</tr>
<tr>
<td>Tail (mm)</td>
<td>119.3 ± 5.3</td>
<td>116.9 ± 6.0</td>
<td>161</td>
<td>-2.68</td>
</tr>
<tr>
<td>Culmen (mm)</td>
<td>17.9 ± 1.6</td>
<td>17.8 ± 1.1</td>
<td>157</td>
<td>-0.29</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>30.4 ± 1.4</td>
<td>30.3 ± 1.3</td>
<td>159</td>
<td>-0.22</td>
</tr>
</tbody>
</table>
Identification of the best parameters for discrimination between sexes

Of the morphological measurements taken, all six were significantly different between the sexes, with males being the larger sex (Table 3.3), as such, the step-wise discriminant analysis was applied to all morphological measurements (excluding weight). Due to the lack of significant differences between ages for most characteristics, and the small magnitude of age-related dimorphism (Table 3.4) compared with sex-related dimorphism (Table 3.3), DFA’s of sex-related dimorphism were performed on the mixed age dataset. This approach is desirable because it results in a more generalised function, and age does not need to be determined in the field. The step-wise procedure was terminated after wing length and total head length were entered, as the change in Rao’s V for the next variable was less than 9.49 (Table 3.5). Accordingly, the step-wise procedure determined the combination of wing length and total head length to be the most discriminating variables between the sexes. These results were supported by the three subsequent re-runs of the analysis with randomised subsamples in each, and was confirmed through manual testing of multiple different discriminant functions (Appendix A.3).

Table 3.5. Step-wise procedure to determine the best variables for developing the discriminant function. For a new variable to be entered, it must satisfy criteria of change in Rao’s V > 9.49, and F > 3.84. The step-wise procedure stopped after the addition of wing length and head length, as the next variable, tarsus length, did not meet criteria for entry.

<table>
<thead>
<tr>
<th>Step</th>
<th>Variables</th>
<th>Next to Enter</th>
<th>F</th>
<th>Rao’s V</th>
<th>Change in V</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>-</td>
<td>Wing length</td>
<td>282.48</td>
<td>282.48</td>
<td>-</td>
</tr>
<tr>
<td>1</td>
<td>Wing length</td>
<td>Head length</td>
<td>61.35</td>
<td>391.48</td>
<td>109</td>
</tr>
<tr>
<td>2</td>
<td>Wing length + Head length</td>
<td>Tarsus length</td>
<td>2.805</td>
<td>397.319</td>
<td>5.84</td>
</tr>
</tbody>
</table>

Discriminant function analyses

A classification function was developed using the full sample of 705 birds to determine the sex of Noisy Miners based on wing length and total head length, with the cut-off value calculated as the weighted average between group centroids (Manly 2004). The function was defined by the equation:

\[
C_1 = (0.148 \times \text{wing length}) + (0.520 \times \text{total head length}) - 44.516
\]
Using this equation, when \( C_1 \) is above the cut off value of -0.324 the individual is classified as male, and as female if it is below. Covariance matrices did not differ between groups (Box’s M test = 1.752, \( F_{3,46838912} = 0.582, p = 0.627 \)) and the data did not display multicollinearity (\( r = 0.387 \)). Both the discriminant function and the subsequent jackknife cross-validation technique correctly assigned sex to 90.0% of individuals (87.1% of 279 females and 92.2% of 371 males). Further, a 50:50 holdout analysis was performed where half the cases were randomly selected to predict the sex of the other half, resulting in 89.8% of individuals being correctly assigned (87.4% of 143 females and 91.7% of 181 males). The equation explained 56% of variation (Table 3.6), and Cohen’s kappa chance correction found the function could predict sex at a rate 79.5% better than chance (Cohen’s kappa = 0.795 ± 0.024 SE, \( p < 0.001 \)).

An alternative classification function using only wing measurements resulted in the equation:

\[
\text{Equation (2)} \quad C_2 = (2.39 \times \text{wing length}) - 32.140
\]

Using this equation, when \( C_2 > -0.264 \) the sex is classified as male, and as female if it is below. Covariance matrices did not differ between groups (Box’s M test = 0.219, \( F_{1,1277648} = 0.219, p = 0.641 \)). This discriminant function and the jackknife cross-validation technique correctly assigned sex to 85.1% of individuals (83.8% of 290 females and 85.1% of 381 males), while the 50:50 holdout analysis correctly sexed 83.0% (81.7% of 142 females and 84.0% of 188 males). The equation explained 48% of variation (Table 3.6), and Cohen’s kappa chance correction found the function could predict sex at a rate 69.7% better than chance (kappa = 0.697 ± 0.028 SE, \( p < 0.001 \)).

<table>
<thead>
<tr>
<th>Function</th>
<th>SCC</th>
<th>Eigenvalue</th>
<th>Wilks Lambda</th>
<th>F</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>( C_1 )</td>
<td>0.56</td>
<td>1.29</td>
<td>0.44</td>
<td>535.79</td>
<td>2, 664</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>( C_2 )</td>
<td>0.48</td>
<td>0.94</td>
<td>0.52</td>
<td>442.27</td>
<td>1, 687</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 3.6. Results of Wilks Lambda, Eigenvalue, and the squared conical correlation (SCC) for the discriminant functions \( C_1 \) and \( C_2 \).

In addition to the common validation techniques used here, the efficacy of using morphological measurements to predict the sex of Noisy Miners was put under further temporal, spatial and inter-observer testing with total head length and wing length as parameters. A discriminant function using measurements from a single site (\( C_{32}; N=124 \)) was used to predict the sex of individuals (\( N=526 \)) from the all other sites, resulting in 88.8% of those individuals being
assigned to the correct sex. Similarly, a discriminant function using measurements from the first removal in August (N=249) were used to predict the sex of individuals removed in September and April (N=401) with 89.5% of individuals being correctly assigned a sex. Lastly, measurements from recorder #1 (JV; N=423, Table 3.1) correctly predicted sex for 85.9% of individuals measured by all other recorders (N=227), and 91.5% vice versa.

3.4 - Discussion

The findings in this study highlight the significant morphological differences between sexes in the Noisy Miner with males being consistently larger than females by 3-10% across all six measurements; weight (10.6%), wing length (6.3%), total head length (4.4%), tail length (3.3%), culmen length (7.7%) and tarsus length (3.1%). The mean measurements recorded in this study and their intersexual variation are consistent with previous findings (Higgins et al. 2001). Despite observing a substantial amount of overlap between the sexes in individual characteristics, we were able to successfully produce a practical multivariate method for sexing the species in the field, without the need for costly molecular or invasive sexing techniques such as laparoscopy (Garcelon et al. 1985; Morrison & Maltbie 1999). The discriminant function analysis correctly assigned sex to 90% of individuals based on total head length and wing length, and 85.1% of individuals based on wing length alone. Both total head and wing length have previously been used successfully in developing discriminant functions for the purpose of sexing passerines (Clarke et al. 2003; Jakubas & Jakubas 2011; Lambert & Blackmore 2015).

Although the discriminant function’s ability to sex Noisy Miners remained highly efficient over small temporal (8 months) and spatial (c. 90km) scales, it is unclear as to how far its range extends, as the size of the species varies latitudinally (Higgins et al. 2001). Furthermore, we cannot be sure that the success of the function developed here extends to the various subspecies (ssp. *titaniota*, ssp. *lepidota*, ssp. *leachi*). The high efficiency of the equation allows it to be used in the field for many purposes, such as studies that require an estimation of a population’s sex ratio, or banders that seek to monitor population demographics over time. However, for purposes where 100 % certainty is required (e.g. behavioural studies), techniques such as molecular sexing are still necessary.
The functions developed in this study were derived from data collected from both immature and mature individuals. Ages were not separated as negligible differences were found between them, particularly when compared with intersex morphometric variation. For this reason, and due to the difficulty in ageing adult-like first immatures in the field, an equation developed from combined ages will likely result in a sexing technique more widely and readily applicable for use in the field (Clarke et al. 2003; Jakubas & Jakubas 2011). Classification rates remained high when functions were tested between observers. In fact, higher classification rates were found when measurements from multiple observers were used to predict the sex of those measured by a single recorder (91.5%), than found when a single observer’s measurements predicted sex from multiple observers’ measurements (85.9%). These results support the inclusion of data from multiple recorders and demonstrate the applicability of the function to field workers.

Sexual dimorphism in birds is common and is developed and maintained by the pressures of natural and sexual selection (Andersson 1994). These pressures are often reflected in life history traits, sex ratios, diets, and social structures, which can further drive and maintain sexual dimorphism. For example, where food is limited, conspecific intersexual competition may be reduced by diversifying feeding habits into segregated niches, resulting in the evolution of morphological variations through natural selection as found in the giant petrel (Hunter 1983; Forero et al. 2005). The factors that maintain sexual dimorphism in the Noisy Miner are unclear, however it is likely a result of the complex cooperative breeding system and social structure that has been well-documented by Higgins (2001).

Noisy Miner colonies often maintain populations with high male to female ratios, reaching up to 2.3 - 3: 1 (Dow 1979b; Arnold et al. 2001). The limited availability of female breeding partners may subject males to increased breeding competition and consequently selection pressure for larger and stronger individuals. Nests are frequently visited by male helpers who provide chicks with food and spontaneously form coalitions to protect nests from intruders through collective mobbing (Arnold 2000; Arnold et al. 2005). Although helpers cooperate to remove threats, unpredictable and hyper-aggressive intraspecific aggression frequently occurs (Dow 1975; Dow 1977, 1978). Fit and strong individuals are more able to meet the high energetic costs that helpers bear, and although the rewards that helpers receive are unclear, it, at the least, increases indirect fitness (Griffin & West 2003; Arnold et al. 2005). Additionally, Noisy Miners exhibit sex-biased hatching sequences in favour of males, which contributes to the larger size of males as the first chick to hatch often receives the greatest parental investment
(Arnold et al. 2001). Parental benefits of raising a male greatly exceed that of raising a female, as male chicks often return as a helper and increase the future reproductive success of parents, providing incentives for larger males to be raised with priority (Clutton-Brock 1991; Koenig & Walters 1999). A quick and easy sexing method could assist researchers in collecting additional information on sex-specific behaviours, and help understand the ecology of this complicated species.

This paper offers a quick and efficient alternative for sexing Noisy Miners in the field, without the need for molecular, invasive, or opportunistic methods. Although there is inherent uncertainty when using discriminant functions to sex birds, this study provides a function that can correctly sex a relatively high proportion of the populations in this study. Moreover, were this equation to be used in conjunction with other techniques, such as identifying gender-specific traits, then classification rates can be further increased. However, considering the current difficulties in sexing the species, were it be used in conjunction with other methods or not, the method proposed here is of high value.
4 - Shifts in demographic structure following removal of Noisy Miners

4.1 - Introduction

Australia is undergoing a period of avifaunal decline, with new species of birds being added to the list of threatened species as their original range sizes decrease due to habitat loss and degradation (Barrett et al. 2007; Ford 2011). Environmental transformations such as land clearing, urbanisation and climate change are becoming increasingly problematic for the future of Australia’s avifauna (Ford et al. 2009; Mac Nally et al. 2009; Ford 2011). The wide range of stressors that affect bird assemblages are becoming more apparent as the situation worsens (Ford et al. 2001). One of these stressors is the highly aggressive Noisy Miner (Manorina melanocephala), a medium sized (~60g) honeyeater endemic to eastern Australia. The Noisy Miner is a cooperative breeder that lives in colonies of up to several hundred birds. They have a complex social structure and are very effective at removing heterospecifics from their territories through intense and persistent group mobbing (Higgins et al. 2001). The species is well known for aggressively protecting its habitat and causing a detrimental impact on resident avifaunal assemblages (Mac Nally et al. 2012).

The Noisy Miner thrives in fragmented open woodlands adjacent to cleared land, particularly in areas consisting of eucalypts with minimal understorey and a high edge-to-area ratio (Higgins et al. 2001; Taylor et al. 2008). Remnant woodland patches throughout eastern Australia, including the extensive network of Traveling Stock Routes (TSR), are often found to be dominated by Noisy Miner colonies. Many hectares of Noisy Miner habitat have hence been created through the long-term and widespread use of traditional European agricultural practices, making Noisy Miners one of the native “winners” of white settlement (Low 2002). Within such habitat the species has been reported to exist in large colonies that can fully and exclusively occupy entire remnant woodland patches (Dow 1977). High-density Noisy Miner colonies greatly reduce the area of available habitat for small birds through the aggressive exclusion of small-bodied heterospecifics, causing a decline in avian diversity where Noisy Miners are present (Grey et al. 1997). The aggressive nature of the Noisy Miner has subjected many threatened species to considerable levels of additional stress; so much so that their hyper-abundance has been recognised by both state (Threatened Species Conservation Act 1995
A key threatening process under the *Environment Protection and Biodiversity Conservation Act 1999* (Cth) is a process that could; a) cause a native species or ecological community to become eligible for inclusion in a threatened list, or b) cause an already listed threatened species or threatened ecological community to become more endangered, or c) adversely affect two or more listed threatened species or threatened ecological communities. Once listed, a key threatening process may be managed with threat abatement plans, however, for a threat abatement plan to be implemented it requires a strategy that is considered a feasible, effective, and efficient way to abate the process. In the case of the Noisy Miner, the development of a threat abatement plan was considered not feasible by the *Threatened Species Scientific Committee* (Threatened Species Scientific Committee 2013).

Although a range of measures exist to mitigate the negative impacts of the Noisy Miner on small woodland birds, they are only feasible at small scales, such as single properties or vegetation remnants. Most strategies focus on habitat modification to increase the structural complexity of woodland patches through revegetation and the promotion of understorey growth (Hastings & Beattie 2006), as structurally complex woodland patches reduce the defensibility of the space by Noisy Miners and provide habitat for small woodland birds. However, even where large-scale habitat modification is effective it may not be feasible, as it could take decades to restore the critical habitat elements upon which small birds depend (Maron *et al.* 2011).

Although a native species, the direct removal of Noisy Miners has been suggested as a more effective strategy to mitigate their negative impacts, being cost-effective and with an immediate, and sometimes long-lasting, benefit to biodiversity (Grey *et al.* 1997; Debus 2008; Mortelliti *et al.* 2016). Culling has been successful in some situations, where little, or no Noisy Miner recolonisation was recorded (Grey *et al.* 1997). However, this is not always the case, as a recent study by Davitt (2016) tested the effectiveness of removals at a larger scale, and found Noisy Miner recolonisation to occur almost immediately. While this study detected an initial positive response by small birds to Noisy Miner removal there was likely to be little, if any long-term benefit to biodiversity (Davitt 2016). The factors that determine the long-term success of culling on Noisy Miners are uncertain, and it is therefore necessary to design experiments that can identify which factors best predict whether culling is likely to be
successful as a threat abatement action, or whether Noisy Miners are likely to recolonise. Additionally, in situations where recolonisation does occur, it would be beneficial to determine where the new population originated from, whether the demographics of the new population resemble that of the old, and whether the new population excludes small woodland birds to the same degree.

The key to an effective threat abatement plan that can mitigate the impacts of the Noisy Miner may lie in the species’ social structure. Complex social structures develop amongst cooperatively breeding birds to allow an individual’s fitness to be greater than were they to mate in single pairs (Koenig 1981; Pöldmaa 1996; Kokko et al. 2001). Consequently, any abrupt changes to age structure or sex ratio are likely to have a negative impact on the efficacy of a cooperatively breeding population. Such changes may have significant implications for threat abatement, as it may provide pathways towards mitigating the impacts of Noisy Miner’s hyper-aggressive colonies.

The boundaries of a colony are hard to identify as they can cover vast areas, and are comprised of many sub-units, known as coteries (Dow 1979b). Coteries are stable units within a colony that consist of around 25 individuals, mainly males, that frequently interact within overlapping activity spaces (Dow & Whitmore 1990). Males are generally the only helping sex within colonies, and this is reflected in the structure of their activity space; male activity spaces overlap widely as they are not territorial, whilst females remain within their own activity spaces, and are aggressively excluded when entering the space of another female (Dow 1979a). This social structure results in philopatric males and displaced females, with the number of females being limited by the area of a colony. Immature females that cannot find space within a colony may be forced to disperse in search of available habitat or another colony with available space. It is common for a sex-bias to occur in these birds, with a bias towards the helping sex in adults (Brown 1987). Consequently, immature females are expected to account for a large proportion of vagrant individuals, as they have the most difficulty establishing an activity space within a colony (Higgins et al. 2001).

This social structure and the consequent displacement of mostly young females into the landscape has implications as to how Noisy Miner recolonisation after culling may occur at such a fast rate. To further our understanding of the mechanisms that facilitate recolonisation, it is necessary to determine whether recolonisation occurs mostly from 1) recolonists comprised of birds that fled the sites while culling was occurring, 2) new individuals moving
in from other parts of the landscape, or 3) colonies/coteries that move into the vacated space. These three alternatives are likely to have different demographic signatures due to the naturally higher occurrence of females within the landscape matrix (matrix, hereafter). As such, measuring the age structure and sex ratio of a newly-established colony may provide a good indication of its source(s) of origin. The aim of this study, therefore, was to examine individuals collected during Davitt’s (2016) study, and evaluate how age structure and sex ratios varied between the original population and subsequent recolonised populations. Specifically, this study tested the following three hypotheses predicted from the published social structure of Noisy Miner colonies:

1) Recolonised populations will have a significantly higher proportion of immatures than were present in the original population,

2) Recolonised populations will have a significantly higher proportion of females than were present in the original population,

3) Recolonised populations will have a significantly lower proportion of mature females that have held a breeding position than found in the original population.

Developing an effective threat abatement plan requires knowledge of how Noisy Miners respond to culling, and in which situations it may be effective. These results will provide information on the structure of the recolonised population and nature of recolonisation, providing insight into the mechanisms that support recolonisation, and how nearby individuals and colonies may react to the sudden release of habitat from an established colony.

4.2 - Methods

Study sites and culling methods

A 12-gauge shotgun was used to remove 1212 individuals from six sites in travelling stock routes (TSRs) located near the town of Fifield in the Western Slopes Bioregion of NSW (-32.808 S, 147.463 E; Fig. 4.1; Appendix B.1). All sites were at least 50 m in width, and ranged between 16 and 49 hectares in area, with an average area of 33.7 hectares (Appendix B.1). Sites were 2 km in length, consisting of two 400-m long survey transects that were separated from each other by 400 m, with an additional 400 m buffer at each end. Removals took place in
August and September 2015 and April 2016. All carcasses were collected and frozen until this study commenced in February 2017.

A trained shooter accompanied by two experienced ornithologists traversed the length of each site by foot, using broadcast of Noisy Miner calls at ~50-100 m intervals to attract Noisy Miners to trees where they could easily be shot. The three personnel (the shooters, hereafter) spread out across the width of each site when walking between playback points to detect, shoot and collect all Noisy Miners encountered. Each site was traversed for between 4.3 and 14.3 hours (spread over 2 days) until the shooters were satisfied that most, if not all, individuals had been removed from the site. In sites in which Noisy Miners were particularly abundant, the shooters initially concentrated on the two survey transects, and cleared the buffers once the transects were clear. Although this study recognises the difficulty in removing an entire colony from a site through direct removal, particularly from habitat within long continuous corridors of TSR’s, the shooters were satisfied that only between one and 10 birds remained on each site after the final day of culling in each removal session.

Figure 4.1. Study sites near Fifield, New South Wales. Treatment sites were subjected to the direct removal (culling) of Noisy Miners during August 2015, September 2015 and April 2016, as described under ‘Study sites and culling methods’. Control sites were not used in this study. Figure taken from Davitt (2016).
**Ageing and sexing birds**

Nine personnel assisted in processing 747 Noisy Miner carcasses from the six sites and three removal events. An attempt was made to balance samples sizes across all sites and removals, although the sample size was limited by the relatively small number of individuals present in sites C45 and C52 in September 2015 (Table 4.1). Each Noisy Miner carcass was examined by dissection to determine sex and age. Gonads were inspected for sex determination, although 22 individuals could not be assigned a sex due to extensive shotgun damage to the gonads. Age determination followed the methods outlined in Chapter 2, with classification based upon the degree of skull pneumatisation and the presence of a bursa of Fabricius, rather than plumage or the undiagnostic shape of the alula. Skull pneumatisation was assessed by peeling back the skin, after making an incision in the crown, and classified as either “minimal”, “partial”, or “complete”. The bursa, an immunosuppressive organ in young birds, was measured and recorded as “present” or “absent”. Lastly, the state of the oviduct was assessed and classed as “straight” or “convoluted”, with convoluted oviducts indicating that the bird had previously laid an egg (Christians & Williams 1999; Vézina & Williams 2003).

<table>
<thead>
<tr>
<th>Removal</th>
<th>C08</th>
<th>C32</th>
<th>C35</th>
<th>C42</th>
<th>C45</th>
<th>C52</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug-15</td>
<td>70</td>
<td>52</td>
<td>50</td>
<td>50</td>
<td>32</td>
<td>31</td>
<td>285</td>
</tr>
<tr>
<td>Sep-15</td>
<td>44</td>
<td>26</td>
<td>42</td>
<td>32</td>
<td>19</td>
<td>18</td>
<td>181</td>
</tr>
<tr>
<td>Apr-16</td>
<td>58</td>
<td>61</td>
<td>48</td>
<td>51</td>
<td>20</td>
<td>43</td>
<td>281</td>
</tr>
<tr>
<td>Total</td>
<td>172</td>
<td>139</td>
<td>140</td>
<td>133</td>
<td>71</td>
<td>92</td>
<td>747</td>
</tr>
</tbody>
</table>

As it is not known at what age the skull of the Noisy Miner becomes completely pneumatised, or at what age the bursa begins to involute, an exact age cannot be determined from these characteristics. They are good candidates for assessing the age of maturity, however, as passerines generally complete pneumatisation by 4-8 months of age (Serventy *et al.* 1967), and the bursa generally involutes by 2-6 months, depending on the species (Glick 1983; Ciriaco 2003). Therefore, for the purpose of this study, all individuals with a bursa were considered first immatures, and classified as “immature”, as were all individuals with minimal or partial skull pneumatisation (Dow 1978). All other individuals were classified as “mature”, recognising that this category may be over-represented as some first immatures may consequently be classed as mature.
This study acknowledges the difficulties and uncertainty associated in ageing this species based on such characteristics, and only applies results as an estimate of the age structure in populations, rather than a definitive assignment of an individual’s age. Further, as this study spans an eight-month period inclusive of the Noisy Miner’s most active breeding period, and seeks to test the effect of removal on the age structure of populations, the results are confounded by the natural and expected influx of immature individuals which would have been recruited between culls.

**Age structure analysis**

Chi-square tests were used to test whether the proportion of immatures differed significantly between removals. Age structure in each removal was initially analysed separately for each of the six sites with a view to pooling sites if they did not differ significantly. Because there was no appreciable breeding activity between August and September 2015, any significant variation in age structure between the first and second removal sessions can be attributed to culling. However, any significant variation in age structure between the August or September 2015 removal and the April 2016 removal is confounded with time because most breeding occurs during spring (Higgins et al. 2001); i.e. any change in age structure due to culling will be confounded with changes due to breeding season.

**Sex ratio analysis**

Fisher’s Exact tests were used to test whether sex ratios differed significantly between removals. Sex ratios were initially tested for significant differences between immature and mature individuals to determine whether separate analyses were necessary. Chi-square tests were also initially used to test whether sex ratios differed significantly between sites, with a view to pooling sites if they did not differ significantly.

Additionally, pairwise Chi-square tests were used to determine whether the sex ratio observed in our study was comparable to the strongly male-skewed sex ratios reported in the literature. For these comparisons we used only the August 2015 sample because the sex ratio observed in subsequent removals was likely to be influenced by culling. To allow cross-study comparisons, this analysis incorporated immature and mature individuals, but did not include nestlings. Data from the six removal sites were pooled for these comparisons.
Analysis of breeding history

Chi-square tests were used to test whether the proportion of mature females with convoluted oviducts differed between removals, and whether the frequency of large follicles (> 1 mm) within oviducts differed between removals. The proportion of mature females with convoluted oviducts in each removal was initially analysed separately for each of the six sites with a view to pooling sites if they did not differ significantly.

4.3 - Results

Age structure analysis

There was a significant difference in age structure (expressed as percentage of immatures) between sites in both the August and September removals (Table 4.2). Accordingly, it was not appropriate to pool sites when comparing age structure between removal sessions. However, for all sites, the proportion of immatures differed significantly between removals, with the third removal consistently having a greater proportion of immatures than previous removals (Fig. 4.2, Table 4.3). The proportion of individuals that were immature ranged between 0 and 25% with a total of 11.9% for the August removal, between 3.1 and 42.1% with a total of 13.81% for the September removal, and between 55.8 and 72.1% with a total of 66.6% for the April removal (Table 4.3).

Table 4.2. Differences in age structure (expressed as percentage immatures) between removal sites in (a) August 2015 removal, (b) September 2015 removal, and (c) April 2016 removal. Age structure differed significantly between sites for both the August and September removal, but not for the April removal in the following year.

<table>
<thead>
<tr>
<th></th>
<th>C08</th>
<th>C32</th>
<th>C35</th>
<th>C42</th>
<th>C45</th>
<th>C52</th>
<th>$\chi^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Aug-15</td>
<td>17.1</td>
<td>25</td>
<td>6</td>
<td>0</td>
<td>9.4</td>
<td>9.7</td>
<td>19.1</td>
<td>0.002</td>
</tr>
<tr>
<td>(n=70)</td>
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<td>(n=50)</td>
<td>(n=50)</td>
<td>(n=32)</td>
<td>(n=31)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Sep-15</td>
<td>20.5</td>
<td>15.4</td>
<td>4.8</td>
<td>3.1</td>
<td>42.1</td>
<td>5.6</td>
<td>21.5</td>
<td>0.001</td>
</tr>
<tr>
<td>(n=44)</td>
<td>(n=26)</td>
<td>(n=42)</td>
<td>(n=32)</td>
<td>(n=19)</td>
<td>(n=18)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c) Apr-16</td>
<td>69</td>
<td>72.1</td>
<td>64.6</td>
<td>70.6</td>
<td>60</td>
<td>55.8</td>
<td>4.07</td>
<td>0.539</td>
</tr>
<tr>
<td>(n=58)</td>
<td>(n=61)</td>
<td>(n=48)</td>
<td>(n=51)</td>
<td>(n=20)</td>
<td>(n=43)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.2. Changes in age structure (percentage immature) between three removal sessions in each of six removal sites. For all sites, there was a significantly higher proportion of immature birds in the April 2016 removal. Sample sizes are shown in Table 4.2, and statistical results in Table 4.3.

Table 4.3. Results of Chi-square tests comparing changes in age structure (percentage immature) between three removals at each of six removal sites. Age structure differed significantly between removals for all sites.

<table>
<thead>
<tr>
<th></th>
<th>Aug-15</th>
<th>Sep-15</th>
<th>Apr-16</th>
<th>$\chi^2$</th>
<th>N</th>
<th>p</th>
</tr>
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<tbody>
<tr>
<td>C08</td>
<td>17.1</td>
<td>20.5</td>
<td>69</td>
<td>43.04</td>
<td>172</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>C32</td>
<td>25</td>
<td>15.4</td>
<td>72.1</td>
<td>35.87</td>
<td>139</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>C35</td>
<td>6</td>
<td>4.8</td>
<td>64.6</td>
<td>57.79</td>
<td>140</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>C42</td>
<td>0</td>
<td>3.1</td>
<td>70.6</td>
<td>75.45</td>
<td>133</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>C45</td>
<td>9.4</td>
<td>42.1</td>
<td>60</td>
<td>15.52</td>
<td>71</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>C52</td>
<td>9.7</td>
<td>5.6</td>
<td>55.8</td>
<td>24.65</td>
<td>92</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Total</td>
<td>11.93</td>
<td>13.81</td>
<td>66.55</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Sex ratio analysis

Sex ratios differed significantly between samples of immature and mature Noisy Miners, with immatures having a significantly higher proportion of females (Fisher’s Exact, $p = 0.009$, N=725; immatures = 51.0% female, n=239; matures = 41.4% female, n=486). Consequently, separate tests were run on immature and mature individuals to assess whether sex ratios differed between removals.
Sex ratios did not differ significantly between sites for immatures (Table 4.4) or matures (Table 4.5) in any of the three removals. However, the sample size for immatures in the August and September removals were small, with at least 20% of cells having an expected count of less than five. Because sex ratios did not differ significantly between sites, data from all sites were pooled to test for significant differences in sex ratio between removal sessions.

**Table 4.4.** Differences in the sex ratio of immatures (expressed as percentage female) between removal sites in (a) August 2015, (b) September 2015 removal, and (c) April 2016 removal. No significant differences in sex ratio was found between sites for any of the three removals. * denotes Chi-square suspect, as at least 20% of cells have an expected count of less than five due to low sample size.

<table>
<thead>
<tr>
<th></th>
<th>C08</th>
<th>C32</th>
<th>C35</th>
<th>C42</th>
<th>C45</th>
<th>C52</th>
<th>$\chi^2$</th>
<th>$p$</th>
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<tbody>
<tr>
<td>(a) Aug-15</td>
<td>54.6</td>
<td>46.2</td>
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<td>0</td>
<td>0</td>
<td>33.3</td>
<td>5.25</td>
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<td>(n=0)</td>
<td>(n=3)</td>
<td>(n=3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Sep-15</td>
<td>44.4</td>
<td>100</td>
<td>50</td>
<td>100</td>
<td>57.1</td>
<td>100</td>
<td>5.07</td>
<td>0.407</td>
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<td>(n=2)</td>
<td>(n=1)</td>
<td>(n=7)</td>
<td>(n=1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c) Apr-16</td>
<td>52.6</td>
<td>51.2</td>
<td>43.3</td>
<td>60</td>
<td>50</td>
<td>50</td>
<td>1.87</td>
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<td>(n=24)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 4.5.** Differences in the sex ratio of matures (percentage female) between removal sites in (a) August 2015, (b) September 2015 removal, and (c) April 2016 removal. No significant differences in sex ratio was found between sites for any of the three removals.

<table>
<thead>
<tr>
<th></th>
<th>C08</th>
<th>C32</th>
<th>C35</th>
<th>C42</th>
<th>C45</th>
<th>C52</th>
<th>$\chi^2$</th>
<th>$p$</th>
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<tbody>
<tr>
<td>(a) Aug-15</td>
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<td>39.5</td>
<td>58.7</td>
<td>51</td>
<td>37.9</td>
<td>29.6</td>
<td>8.96</td>
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<td>(n=46)</td>
<td>(n=47)</td>
<td>(n=29)</td>
<td>(n=27)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Sep-15</td>
<td>51.4</td>
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<td>36.8</td>
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<td>36.4</td>
<td>31.3</td>
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<td>(c) Apr-16</td>
<td>41.2</td>
<td>25</td>
<td>29.4</td>
<td>14.3</td>
<td>25</td>
<td>47.4</td>
<td>5.34</td>
<td>0.376</td>
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<tr>
<td>(n=17)</td>
<td>(n=16)</td>
<td>(n=17)</td>
<td>(n=14)</td>
<td>(n=8)</td>
<td>(n=19)</td>
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Immature individuals displayed sex ratios that did not differ significantly from parity in August ($\chi^2 = 1.48$, N=33, $p = 0.223$), September ($\chi^2 = 1.50$, N=24, $p = 0.221$) and April ($\chi^2 = 0.198$, N=182, $p = 0.657$) (Fig. 4.3). Mature individuals displayed a significantly male-biased sex ratio in August ($\chi^2 = 3.95$, N=243, $p = 0.047$) and April ($\chi^2 = 12.0$, N=91, $p < 0.001$), whilst the sex ratio in September was not significantly different from parity ($\chi^2 = 2.63$, N=152, $p = 0.105$) (Fig. 4.3). However, the lack of a significant difference from parity in September is likely to be due to low statistical power, as a result of small sample size, because the sex ratio was equal
to that observed in August. There was no significant difference in sex ratios between the first and last removal for immatures (Fisher’s Exact, $p = 0.256$, $N=215$; Fig. 4.3), however, matures had a significantly greater proportion of males in the last removal when compared with the first (Fisher’s Exact, $p = 0.033$, $N=334$; Fig. 4.3).

**Figure 4.3.** Sex ratios for each of the three removal trips, separated by age. No significant differences were found in sex ratios between removals for immatures, however, matures had a significantly greater proportion of males in the April removal when compared with the August removal.

To allow cross-study comparisons of sex ratio, only samples of the immature and mature Noisy Miners from the August 2015 removal session were used in the analysis. Sex ratios did not differ between sites for any of the three removals (Table 4.6). Because sex ratios did not differ significantly between sites, data from all sites were pooled to test for significant differences in sex ratio between studies.

**Table 4.6.** Differences in the overall sex ratio (percentage female) between removal sites in the August 2015 removal. No significant differences in sex ratio was found between sites.

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<th>C45</th>
<th>C52</th>
<th>$\chi^2$</th>
<th>p</th>
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<tbody>
<tr>
<td>Aug-15</td>
<td>40.3</td>
<td>41.2</td>
<td>55.1</td>
<td>51.1</td>
<td>34.4</td>
<td>30</td>
<td>7.48</td>
<td>0.188</td>
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<tr>
<td></td>
<td>(n=67)</td>
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<td>(n=47)</td>
<td>(n=32)</td>
<td>(n=30)</td>
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Although the overall sex ratio from the initial August removal was significantly male-biased at 1.32:1 ($\chi^2_1 = 5.23$, $N=276$, $p = 0.022$; Male: 157, Female: 119), it was significantly less than
the sex ratios reported in other studies \( (\chi^2_3 = 13.28, \text{N}=789, p = 0.004; \text{Fig. 4.4}) \). Pair-wise tests confirmed that the sex ratio found in this study was significantly less than those reported by Barati (2017; Fisher’s Exact, \( p = 0.003, \text{N}=564 \)), Arnold et al. (2001; Fisher’s Exact, \( p = 0.004, \text{N}=457 \)), and Dow (1978; Fisher’s Exact, \( p = 0.047, \text{N}=320 \)).

![Bar Chart](image)

**Figure 4.4.** Comparison of sex ratio (expressed as number of males per female) between this study and three other studies. The sex ratio found in this study is significantly less than reported by Barati (2017), Arnold et al. (2001), and Dow (1978). * values reported for Dow’s 1978 study are averaged from data collected in Laidley during June and November 1972. See text for statistical tests of significance.

**Analysis of breeding history**

The proportion of mature females with convoluted oviducts did not differ between sites (Table 4.7) in any of the three removals. However, the sample size for mature females in the September and April removals were small, with at least 20% of cells having an expected cell count of less than five. Consequently, samples from each site were pooled for analysis of changes in the proportion of mature females with convoluted oviducts between removal sessions.

The proportion of mature females with convoluted oviducts differed significantly between removals \( (\chi^2_2 = 6.157, \text{N}=185, p = 0.046) \). The proportion of mature females with convoluted oviducts increased over removals, with 59.4% (N=96), 72.1% (N=61) and 82.1% (N=28) of mature females displaying convoluted oviducts in the August, September, and April removals, respectively (Fig. 4.5).
Table 4.7. Differences in the proportion of mature females with convoluted oviducts (expressed as percentage convoluted) between removal sites in (a) August 2015, (b) September 2015 removal, and (c) April 2016 removal. No significant differences in the proportion of mature females with convoluted oviducts was found between sites for any of the three removals. * denotes Chi-square suspect, as at least 20% of cells have an expected count of less than five due to low sample size.

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<th>(\chi^2)</th>
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<tr>
<td>(a) Aug-15</td>
<td>52.6</td>
<td>27.3</td>
<td>66.7</td>
<td>75</td>
<td>45.5</td>
<td>71.4</td>
<td>9.32</td>
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<td></td>
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<td>(n=24)</td>
<td>(n=24)</td>
<td>(n=11)</td>
<td>(n=7)</td>
<td></td>
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<tr>
<td>(b) Sep-15</td>
<td>56.3</td>
<td>62.5</td>
<td>85.7</td>
<td>78.6</td>
<td>100</td>
<td>60</td>
<td>5.86</td>
<td>0.320</td>
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<td></td>
<td>(n=16)</td>
<td>(n=8)</td>
<td>(n=14)</td>
<td>(n=14)</td>
<td>(n=4)</td>
<td>(n=5)</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>(c) Apr-16</td>
<td>83.3</td>
<td>75</td>
<td>60</td>
<td>100</td>
<td>100</td>
<td>88.9</td>
<td>2.97</td>
<td>0.705</td>
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<td></td>
<td>(n=6)</td>
<td>(n=4)</td>
<td>(n=5)</td>
<td>(n=2)</td>
<td>(n=2)</td>
<td>(n=9)</td>
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Figure 4.5. Proportion of mature females with convoluted oviducts for each of the three removals. The proportion of mature females with convoluted oviducts differed significantly between removals. See text for statistical tests of significance.

Lastly, although the proportion of mature females with large follicles differed between sites in August and April (Table 4.8), it was largely a result of the inadequate sample size for mature females, with at least 20% of cells having an expected cell count of less than five. Consequently, samples from each site were pooled for analysis of changes in the proportion of mature females with convoluted oviducts between removal sessions. This analysis included mature females with an unidentified oviduct condition, as follicles would have remained noticeable in such cases.
The proportion of mature females with large follicles differed significantly between removals ($\chi^2 = 12.925, N=201, p = 0.002$). The proportion of mature females with large follicles was highest in the September removal, with 7.6% (N=106), 24.2% (N=66) and 3.5% (N=29) of mature females displaying large follicles in the August, September, and April removals, respectively (Fig. 4.6). Furthermore, when only individuals with convoluted oviducts were analysed, these proportions changed to 7.0% (N=57), 36.4% (N=44) and 4.4% (N=23), and remained significantly different between removals ($\chi^2 = 18.382, N=124, p < 0.001$).

**Table 4.8.** Differences in the proportion of mature females with large follicles (expressed as percentage with large follicles) between removal sites in (a) August 2015, (b) September 2015 removal, and (c) April 2016 removal. Significant differences in the proportion of mature females with large follicles was found between sites for August and April, although largely a result of inadequate sample size. * denotes Chi-square suspect, as at least 20% of cells have an expected count of less than five due to low sample size.

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<th>C45</th>
<th>C52</th>
<th>$\chi^2$</th>
<th>p</th>
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<tbody>
<tr>
<td>(a) Aug-15</td>
<td>0.00</td>
<td>26.67</td>
<td>3.70</td>
<td>0.00</td>
<td>27.27</td>
<td>0.00</td>
<td>18.90</td>
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</tr>
<tr>
<td>(b) Sep-15</td>
<td>16.67</td>
<td>30.00</td>
<td>28.57</td>
<td>20.00</td>
<td>25.00</td>
<td>40.00</td>
<td>1.70</td>
<td>0.892</td>
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<td>(n=14)</td>
<td>(n=15)</td>
<td>(n=4)</td>
<td>(n=5)</td>
<td>*</td>
<td></td>
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</tr>
<tr>
<td>(c) Apr-16</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>50.00</td>
<td>0.00</td>
<td>14.00</td>
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<td>(n=4)</td>
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<td>(n=2)</td>
<td>(n=2)</td>
<td>(n=9)</td>
<td>*</td>
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**Figure 4.6.** Proportion of mature females with large follicles for each of the three removals. The proportion of mature females with large follicles differed significantly between removals. See text for statistical tests of significance.
4.4 - Discussion

Recolonised populations were expected to contain a higher proportion of immatures and females, and a lower proportion of mature females with convoluted oviducts, when compared with the original population. However, the proportion of immature individuals in the recolonised September population did not differ from the August (original) population, and, although the recolonised April population contained a significantly higher proportion of immatures when compared with the original population, it was confounded by the breeding season. There was no significant difference in the sex ratio of immatures between the original population and the recolonised April population, and there were significantly fewer matures females in the recolonised April population when compared with the original population. Lastly, the proportion of mature females with convoluted oviducts were significantly higher in both recolonised populations when compared with the original population.

4.4.1 - Age structure of recolonising Noisy Miners

Although the September population’s age structure remained similar to the original, the recolonised April population consisted of a significantly higher proportion of immatures. The original population consisted of around 12% immature individuals in August 2015, the following removal trip in September 2015 found a similar proportion of around 14% immatures, and the final removal trip in April 2016 found a population consisting of around 67% immatures. The similar proportion of immatures found in the August and September 2015 removal were not expected, as it was hypothesised that most recolonisation would be driven by vagrant immatures within the matrix. However, as the first removal was long after the previous year’s spring, when most breeding occurs, and before the height of breeding season in 2015, it is plausible that; a) not many vagrant immatures remained in the matrix, as they either died or found space within another colony earlier in the year, and b) neighbouring colonies, or coteries, may spread out during breeding season to increase the average quality of available nesting sites and per capita population growth (Krüger & Lindström 2001; Kokko et al. 2004). The latter explanation is supported by our data, because the age structure was similar between the August and September removal events, and the density of Noisy Miners was indeed seen to reduce from an average of 1.82 birds/ha to 1.47 birds/ha (Appendix B.1).
Additionally, the proportion of known immatures in Dow’s (1978) Noisy Miner population was found to be 11% at the beginning of breeding season in 1972, similar to the population found in September, suggesting recolonists likely derived from immigrating colonies or coteries, rather than vagrant individuals.

The sharp increase in the proportion of immatures found in the April 2016 removal is of greatest interest. It is highly unlikely that the April population, consisting of 67% immature individuals, represented a colony’s natural age structure, rather, it appears that younger birds were over-represented. Although the increase is largely confounded by the previous breeding season, long-lived, colonial Australian honeyeaters are not generally found with such a high proportion of immatures in established colonies. The closely related cooperatively breeding Bell Miner exhibited an annual mean age structure of only 20% to 45% immatures (0-8 months old), surveyed on average 13.1 times per month between 1982 and 1987, however it likely fluctuated widely between seasons (Clarke & Heathcote 1990).

Furthermore, data averaged from Dow (1978) allows approximate comparisons of our results to the age structure of a natural Noisy Miner colony. Dow’s (1978) Laidley site supported an average of 56 individuals in 1972 with a sex ratio of 2.2:3.3:1 (approximately 18 females). Females built 53 nests during this time and had an average clutch size of around 2.6 eggs. With around 75% of nests being laid in, it is feasible that 103 eggs were laid throughout the year, of which only 11 individuals fledged. The nest success and the likelihood of an egg producing a fledgling was very low at around 10%. Furthermore, the influx of new fledglings would hence only account for around 17% of the population, far less than the average of 67% found in April throughout our sites (Dow 1979a). Therefore, it is reasonable to conclude that the majority of immatures found in April throughout our sites were recolonists from other parts of the landscape, rather than native to the site.

These findings resulted in the rejection of this study’s first hypothesis: Recolonised populations will have a significantly higher proportion of immatures than were present in the original population. However, the effect of the breeding season on the availability of vagrant immature individuals within the matrix was underestimated. Because Noisy Miners breed year-round (Higgins et al. 2001), it was thought that immature individuals would be available within the matrix in relatively consistent numbers throughout the year, and hence would act as recolonists regardless of the time of cull. Instead, it may be the case that the majority of recolonists will
only be immature individuals during or following breeding season, when they are abundant within the matrix.

4.4.2 - Sex-ratio of recolonising Noisy Miners

Immatures were found to have sex ratios not significantly different from parity across all removals, however, sample sizes were low amongst the August and September removal session. Matures had a significantly male-bias sex ratio in the August 2015 and April 2016 removals, but a sex ratio not significantly different from parity in the September 2015 removal, although this was likely due to low statistical power as the sex ratio was equal to that observed in August. This study found no differences in sex ratios between removals for immatures, and a significantly greater proportion of mature males in April 2016, when compared with previous removals. Because the sex ratios of recolonists were significantly different between samples of immature and mature Miners, and responded differently to culling, it is necessary to discuss the results for each separately.

Immatures

The even sex ratios found amongst immatures are likely a remnant of the even primary/nestling sex ratios found in the species before the male-bias develops through the high occurrence of female displacement (Arnold et al. 2001; Higgins et al. 2001; Barati 2017). Whilst it is unclear at what age female-biased displacement occurs, it likely takes place as they approach breeding age and begin to search for breeding positions, which could occur between 8-12 months of age (Clarke & Heathcote 1990; Higgins et al. 2001). The Bell Miner exemplifies this as the mean age of dispersal is 8 months, close to the minimum observed age-of-first-breeding for both males (8.3 months) and females (9.7 months) (Clarke 1988; Clarke & Heathcote 1990).

However, because the vast majority of immatures must have immigrated into the sites, it seems both male and female immatures are choosing to disperse from colonies at an earlier age, and at the same rate. Whilst females usually disperse more often than males due to mother-daughter breeding competition (Clarke & Heathcote 1990), male dispersal may also be substantial, as it is beneficial to avoid the deleterious effects of
inbreeding, and to gain fitness benefits (Woolfenden & Fitzpatrick 1978; Koenig & Pitelka 1979; Greenwood & Harvey 1982). Male dispersal may result in greater fitness benefits than remaining as a philopatric helper in the absence of ecological constraints (Woolfenden 1989), which, in territorial species, is often hypothesized to be the saturation of suitable habitat by sedentary established groups (Koenig 1981; Emlen 1982; Stacey & Ligon 1987). Because young birds are often excluded from optimal habitats amongst communal species, they may take any opportunity to occupy vacant sites when they arise (Smith 1978). As such, when habitat is suddenly vacated following culling, immatures of both sexes may benefit equally from establishing a position within it.

Natal dispersal from nearby colonies may be particularly prevalent in this scenario due to the immediate and large-scale release of productive habitat. It is likely that immature individuals could identify the vacant habitat whilst performing social activities such as long-flights (Dow 1975), foraging, or chasing intruders, and possibly during what would be the short-term transient dispersals that act as a precursor to successful permanent dispersal, as seen in other cooperative breeders (Gaston 1978; Lewis 1982; Clarke & Heathcote 1990). The discovery of suitable vacant habitat, and the subsequent opportunistic dispersal, could be rapid as Noisy Miners live in open woodlands where they can efficiently maintain a watch over neighbouring habitat as they survey their territorial boundaries (Brown 1964; Kiester & Slatkin 1974; Woolfenden & Fitzpatrick 1978).

**Matures**

Mature individuals reacted quite differently to culling. Although the September population supported a sex ratio equal to that observed in the initial August population, the April population exhibited a significantly different sex ratio, with a lower proportion of females than found in previous removal sessions. The unchanged sex ratio amongst matures in September suggests that there was an equally rapid movement of mature individuals of both sexes, proportional to their original respective abundance, into suitable vacant habitat. Alternatively, the unchanged demographics could be explained by recolonists that fled during culling, however this is unlikely (see *What is the source of recolonists?*, below). A more likely explanation of this type of recolonisation is that
nearby colonies or coteries were shifting or extending their boundaries to incorporate the newly vacated habitat, rather than vagrant individuals, or individuals that fled during culling, acting as recolonists. However, it is likely that the matures that moved into the habitat were not only subordinate “floaters” that could not previously establish a breeding position (see Analysis of breeding history, below), whom would be expected to make up the majority of mature recolonists (Smith 1978).

The decreased proportion of mature females in the April population may have been caused by the influx of individuals and the consequent increase in Noisy Miner density within the habitat, resulting in increased breeding competition between mature females, and hence a higher occurrence of mature females being displaced. This could be the case, particularly because individuals within the April population had a longer time (~7 months) to properly establish breeding positions, social hierarchies and territories, than individuals within the September population (~3 weeks). The sex ratios of the April population imply that either colonies, coteries or vagrant individuals moved into the habitat and subsequently excluded females from the newly established population. However, recolonists are less likely to have originated from the matrix, where more females than males are thought to exist, because, the frequency of female exclusion would need to be far higher than observed in any of our populations to result in the significantly increased male-bias.

These results were not expected, as it was thought that the majority of recolonisation would occur from females, which was not the case for any samples of immature or mature recolonists. These findings resulted in the rejection of this study’s second hypothesis: Recolonised populations will have a significantly higher proportion of females than were present in the original population. However, this may have been at least partially due to the high proportion of females within the original sites, because although we observed a significantly male-biased sex ratio of 1.32:1, it was significantly less than the 2.1-3.3:1 male-bias reported by Barati (2017), Arnold et al. (2001) and Dow (1978). The uncharacteristically high proportion of females within colonies suggests that there was less pressure on female dispersal within our study site than would be expected based on the literature. Furthermore, the reduced occurrence of female displacement would affect the demography of individuals within the matrix, resulting
in less vagrant females than would be expected in areas with colonies that support a greater male-biased sex ratio.

It is unclear whether this sex ratio was a result of infrequent female dispersal, or frequent male dispersal, but both present plausible explanations. If the surrounding habitat is not saturated, and there exists vacant breeding spots, females may disperse throughout the habitat relatively unchallenged, and would undoubtedly be followed by males seeking to breed. It is when suitable habitat reaches the point of saturation whereby females are subjected to high levels of displacement from other females, and males gain more benefit from remaining as philopatric helpers than would be gained by dispersing into an already-saturated landscape (Brown 1974; Emlen 1982). It is this scenario that drives the strong male-biased sex ratios found in other colonies, and the consequently expected high proportion of females wandering throughout the matrix. This study did not measure the extent of occupied territory throughout the study sites, and hence cannot determine with confidence the degree of habitat saturation. However, to explore this further for the purpose of this study, a comparison of adult sex ratio with the estimated density of Noisy Miners should provide an adequate indication of the degree of habitat saturation, given that they are highly correlated (Brown 1974).

Here, population densities were estimated independently for each site by totaling all birds shot within the respective removal session and calculating the area of each site, which was 2000m in length and at least 50m in width (Appendix B.1). The study area chosen was not representative of a colonial boundary, nor the entirety of any population, rather it was an arbitrarily chosen site containing suitable Noisy Miner habitat, Noisy Miners, and a TSR width greater than 50m. The original populations removed from our sites supported Noisy Miner colonies with densities ranging between 0.9 and 2.8 birds/ha, with an average of 1.8 birds/ha and an adult male-biased sex ratio of 1.29:1 (N=243). Our study sites in April had a higher density of Noisy Miners than the original populations, ranging between 0.6 and 4.6 birds/ha, with an average of 3.1 birds/ha, and exhibited an adult sex ratio of 2.14:1 (N=91), more representative of the values reported in previous studies (Dow 1978; Arnold et al. 2001; Barati 2017). The density of birds almost doubled between the August and April removals, which may have increased breeding competition amongst females. An increase in breeding competition would result in the displacement of more females, whilst activity space for males would remain available. This relationship is supported by Dow’s 1978 study, as it reported populations with a density of 8.1 birds//ha and an adult male-biased sex ratio of 3.3:1 in June 1972, followed by a density of 7.7 birds/ha and an adult male-biased sex ratio of 2.2:1 in
November 1972 within the same site. However, it is important to note that the calculation and accuracy of reported densities may have differed between studies, because, although Dow studied a fixed, arbitrarily selected site, it only comprised of seven hectares, and Miners were surveyed within 50m each side of a designated route, rather than shot. Regardless, these findings suggest that low-density Noisy Miner colonies may exhibit low male-biased sex ratios due to the low levels of habitat saturation and consequent lack of breeding competition amongst females, whilst high-density Noisy Miner colonies may result in highly male-biased sex ratios through increased habitat saturation and the consequently frequent displacement of females.

4.4.3 - Analysis of breeding history

The analysis of breeding history was conducted using only mature females, where convoluted oviducts indicate that the female had previously held a breeding position, and large follicles indicate they were in the process of laying an egg. Over half of all females in the original population had convoluted oviducts, suggesting that the populations remained functional with such a high proportion of females. The proportion of convoluted oviducts increased from 59.4% in August to 72.1% in September, and finally to 82.1% in April. The proportion of females with large follicles increased from 7.6% in August to 24.2% in September, before decreasing to 3.5% in April.

The increased proportion of convoluted oviducts following removal suggests that the majority of mature female recolonists in the area at the time have at some point controlled a breeding position within a coterie for at least one breeding season. It is likely, then, that the mature individuals that colonised were not just subordinates from previous years that could not establish their own activity space, because, if that were the case, we would expect to see a reduced proportion of convoluted oviducts, representative of individuals that could not establish a breeding position. For mature breeders, a competitive advantage may be gained from relocating to lower density habitat where a larger activity space can be claimed, and an individual’s chances of successful reproduction are increased (Reiter et al. 1981). This has been seen in another cooperatively breeding species, the acorn woodpecker (Melanerpes formicivorus), which was found to claim a territory size per breeding unit that was correspondingly higher in areas with lower density (Trail 1980). However, dispersal is often very rare amongst individuals that had previously held breeding status, as found for the
cooperative breeding Bell Miner (*Manorina melanophrys*) and the communal Kittiwake, (*Rissa tridactyla*) (Wooller & Coulson 1977; Clarke & Heathcote 1990).

Alternatively, it may be the case that the majority of recolonists were in fact subordinate floaters that were adopting a “patient strategy”, whereby individuals avoid or delay dispersal while waiting for a breeding vacancy (Emlen 1982; Brown 1987; Clarke & Heathcote 1990). This could be the case, given that it can take only 6.5 days for a female to build a nest and lay its first egg (Dow 1978), and there was approximately three weeks between the August and September removal sessions, and seven months between the September and April removal sessions. It is feasible, therefore, that females that had not previously held breeding positions had time to; opportunistically disperse to the vacant habitat, claim an activity space, mate, build a nest, and lay an egg. The dispersal of females would likely be followed by subordinate males that were acting as helpers, as they would benefit from a higher chance to sire offspring in new habitat with a lower male density.

Our results support this alternative explanation, as the mature females in September had a significantly increased proportion of large follicles (24.2%) when compared with August (7.6%), which suggests that many more individuals were in the process of laying eggs. The increased proportion of birds with large follicles was not only due to breeding season, as we would have expected similar proportions in August, but rather that a kind of “breeding frenzy” was occurring. Furthermore, over a third (36.4%) of females with convoluted oviducts exhibited large follicles, meaning that the larger proportion of birds found with convoluted oviducts may well have been explained by the opportunistic dispersal and rapid breeding of individuals that could not establish a breeding position within their previous colony or coterie. However, it remains unlikely that all individuals without large follicles had also had time to lay their first egg within the new habitat. Additionally, the low proportion of large follicles (3.5%) amongst the mature females seen in April, coupled with their significantly higher proportion of convoluted oviducts (82.1%) suggests that breeding behaviour had returned to normal after the seven months since last removal, although this is confounded by the end of breeding season.

These results ultimately led to the rejection of our third and final hypothesis: *Recolonised populations will have a significantly lower proportion of mature females that have held a breeding position than found in the original population*. Instead, the increased proportion of convoluted oviducts and large follicles found amongst September’s recolonists suggest that; a)
there is immigration of a substantial number of breeding individuals from other colonies/coterie, and b) subordinate “floaters” rapidly identify and immigrate into suitable vacant habitat where they can immediately establish a breeding position.

4.4.4 - What is the source of recolonists?

The demography of vagrant individuals would have undoubtedly been affected by the low level of female displacement, causing the demographic signatures of recolonised populations to be similar between populations originating from individuals in the matrix and whole colonies, particularly outside of breeding season. As such, the demographic signatures of the recolonised populations offer an ambiguous view of the source of recolonisation. Regardless, it seems that the source of recolonisation certainly differed between the September and April populations.

September’s unchanged demographics could be explained by recolonists that fled the site during shooting, however, this is unlikely as it cannot explain the large number of individuals that were present. Wandering individuals in the landscape could be responsible for the quick recolonisation, although, at least a slightly greater proportion of females would have been expected, which did not occur. The population could be better explained by a neighbouring colony, or coterie, shifting or extending their boundaries, perhaps to afford females more space and resources before the height of breeding season. This type of recolonisation is supported by the increased proportion of convoluted oviducts and large follicles amongst the mature females. The high frequency of birds with large follicles present suggests that immediately after the August cull there was an influx of subordinate females that may not have been able to previously establish their own activity space. The rapid recolonisation and subsequent breeding is typical of opportunistic floaters that may have been forced to adopt a “patient strategy” (Emlen 1982; Brown 1987). However, because over 60% of females with convoluted oviducts did not exhibit large follicles, it is likely that many of them had held a breeding position in a previous breeding season. Immigrating breeders may have chosen to disperse for a competitive advantage within a new low-density colony where they may be able to claim a larger activity space (Trail 1980). Ultimately, the type of recolonisation seen in September was most likely driven by neighbouring colonies shifting or extending their boundaries, comprising of a combination of subordinate floaters who ceased the opportunity to
establish a breeding position, and mature breeders seeking larger activity spaces for a competitive advantage.

Although the April population was confounded by breeding season, the large proportion of immatures was greater than could be explained by a colony’s natural age structure, suggesting that new individuals were moving in from the matrix or surrounding colonies. There were two interesting findings amongst their sex ratios; a) immatures had sex ratios no different from parity, and b) matures had a significantly lower proportion of females than in previous removals. The even sex ratios amongst immatures is a particularly important finding, as it reflects the even primary sex ratios of nestlings. A significant proportion of these immature recolonists may have derived from the matrix, as the sex ratio of displaced immatures could well be close to parity. However, most immatures were likely still too young to be excluded, as they may not have been close to the age-of-first-breeding. Rather, the mechanism that drove their recolonisation was likely their choice for early natal dispersal into productive habitat with vacant breeding positions. The large-scale release of suitable habitat would have reduced habitat saturation considerably, increasing the chances of successful natal dispersal, and making it a feasible and effective strategy for both sexes. The low proportion of mature females may have suggested an increasing pressure on female exclusion, which could be due to the increased density of Miners within the habitat and the consequent increase in breeding competition. More importantly, however, it suggests that mature individuals were moving in from nearby colonies, as the level of female exclusion would have needed to be far too high to suggest matures were recolonising from the matrix.

The abundance of females throughout our study site, and the study’s inclusion of breeding season within its timeframe resulted in data that was difficult to interpret, and genetic testing may be required to provide the information necessary to solve many of the challenges faced in this study. These results indicate that there may be some additional factors that determine the pathways to recolonisation that had not been foreseen. The time of cull may have a large influence on how a cleared area is recolonised by Noisy Miners, as the demographic structure of recolonised populations is dependent on the demography of the available individuals/colonies in the surrounding landscape. For example, were a colony to be culled following spring, when an abundance of immatures and females are likely to be available, the recolonised populations may comprise a large proportion of immature females. Alternatively, were a colony to be culled during autumn, when fewer immature individuals exist in the matrix, the recolonised population may comprise a similar age structure to the original. This could
result in an autumn cull being followed by a slower recolonisation than a spring cull, as immature individuals in the matrix would have already perished or found a place within another colony.

4.4.5 - Future directions

Whilst we were able to draw important information from the data available, there was inherent uncertainty that may have caused some significant relationships to be overlooked. This study was limited by the breeding season that occurred between removals, because our results were largely confounded by the consequent influx of immatures which made it difficult to determine the effect of culling on the age structure of recolonised populations. Further, the experiments that provided the data for this study were not designed for the purpose of this study, resulting in controls that were not conducive to our aims. The known difficulty in ageing this species, even when using internal characteristics, created some inherent errors in the classification of mature individuals and likely led to it being an over-represented category. Furthermore, age may be a misleading category as the age-of-first-breeding is not known for the Noisy Miner, and hence sexual/social maturity might occur before physiological maturity.

Future studies focussed on how culling influences the demography of recolonised populations can eliminate this uncertainty by conducting research outside of breeding season, and implementing genetic testing. Alternatively, if breeding season is incorporated within the study’s duration, control sites should be subject to the final removal treatment to allow comparisons between the effect of culling and the effect of breeding season on the demography of Noisy Miner populations. Such studies should focus their efforts on populations that exhibit a strong male-bias, because the demographic signatures of recolonised populations would be clearly defined between the different types of recolonisation, allowing a greater understanding of how recolonisation occurs and whether the type of recolonisation changes between seasons. Additionally, future studies should seek to investigate whether the social system of Noisy Miner populations differs between thin contiguous remnant patches and larger isolated remnant patches. Specifically, studies focussing on how colonies and coteries form, interact, and disperse throughout linear habitats. Results from such studies may shed light on how dispersal and spacing behaviour, social systems and sex ratios of Noisy Miners adapt to modified environments.
5 - Summary and Conclusions

The detrimental impacts of the Noisy Miner’s hyper-aggressive colonies have become a focal point amongst the challenges faced by Australia’s woodland avifauna. Available habitat in the landscape has been severely reduced through the combined effects of anthropogenic landscape change and Noisy Miner domination. Consequently, many threatened species of birds are at further risk of becoming endangered, while the critically endangered Regent Honeyeater (*Anthochaera Phrygia*) and the endangered Swift Parrot (*Lathamus discolor*) are at an increased risk of becoming extinct (Higgins *et al.* 2001; Saunders & Heinsohn 2008). The biodiversity threat posed by the Noisy Miner has resulted in their classification as a Key Threatening Process (KTP), by both state (*Threatened Species Conservation Act 1995* (NSW), listed 27 September 2013) and federal legislation (*Environment Protection and Biodiversity Conservation Act 1999* (Cth), listed 7 April 2014). Although state and federal law officially recognises the magnitude of this issue, a feasible, effective and efficient threat abatement plan could not be developed for the KTP. However, the abundance of small birds throughout the landscape will continue to decline if Noisy Miners are not managed effectively.

Various threat abatement strategies have been attempted, with the most successful involving habitat modification and the direct removal (culling) of Noisy Miner colonies from woodland patches. Habitat modification focusses on increasing the structural complexity of the understorey and creating ecological niches that provide protection from Noisy Miners. Although this method seems ethically and ecologically superior to culling, it cannot feasibly be scaled up to a state or national scale due to the immense time and resources it would require to be implemented successfully. Alternatively, culling is a quick and efficient method that immediately removes all Noisy Miners from an area and releases the habitat to other small birds. Furthermore, this method can be scaled up and easily adopted by land owners. Culling has been successful in some situations, where no Noisy Miner recolonisation has been recorded (Grey *et al.* 1997). However, a recent study has found this method to be ineffective when compared with this previous work, because it was immediately followed by Noisy Miner recolonisation (Davitt 2016). This raises multiple questions, 1) under what conditions is culling an effective long-term strategy, 2) what habitat characteristics best predict the occurrence of recolonisation, and 3) how does recolonisation occur?
The aim of this study was to increase our understanding of how Noisy Miner recolonisation occurs following the direct removal of an entire colony from larger areas of woodland habitat. In particular, this study focussed on investigating whether recolonists were derived from individuals within the landscape’s matrix, neighbouring colonies, or individuals that had fled during culling. Information regarding the source of recolonists would further our understanding of what facilitates recolonisation, and assist in the development of best practice management for the effective culling of abundant Noisy Miner colonies.

This study was made possible through the use of carcasses that were collected as part of a wider experiment investigating the restoration of woodland bird communities by culling of Noisy Miner populations (Davitt 2016). The study removed Noisy Miners from six sites on three separate occasions, giving me the opportunity to assess how the demographic characteristics of populations changed after culling. Investigating changes in demography would provide an insight into the origin of recolonists, based on the social structure of Noisy Miner colonies and the frequent displacement of females into the matrix. For this study to be successful, it was necessary that birds were sexed and aged. Whilst doing so, there was opportunity to test the efficacy of a current ageing technique, as well as develop a sexing equation, to assist future researchers in sexing and ageing birds in the field.

Noisy Miners, with the exception of juveniles, are particularly difficult to age in the field because they show no distinct differences between ages in plumage or eye-patch colour. Many researchers have had to rely on alternative methods of ageing, such as the shape of the longest feather of the alula, to age the species. A sharp and thin alula was thought to indicate mature individuals, whilst a round and wide alula was thought to indicate an immature individual. However, through the critical analysis of this relationship we found this to be an unreliable method of ageing, and for it to be used with caution, particularly for age-sensitive studies. It is also difficult to distinguish between male and female Noisy Miners, as they are monochromatic and relatively similar in size. Previously, researchers have relied on sighting gender-specific activities or behaviours amongst banded birds to assign a sex, however, this is not always possible, or reliable. Through the application of multivariate statistical analyses on the morphological characteristics of Noisy Miners, we were able to produce an equation that could correctly assign sex to 90% of individuals. As Noisy Miners become an increasingly large threat to avifaunal assemblages, it is important for researchers to have access to reliable sexing methods that can facilitate ecological studies.
The main objective of this study, however, was not the ability to sex Miners in the field, or the cautioning of a current ageing technique, but to gain insights into the demography of recolonised populations, particularly with comparison to the original population. The first important finding was the unexpectedly high proportion of females within the original populations. We found an anecdotal correlation between the proportion of females and the density of Noisy Miners within a population. The original population comprised of a high proportion of adult females, whilst the final recolonised population found in April comprised of a lower proportion of adult females, and a higher density of Noisy Miners. The initial low sex ratios would have undoubtedly caused flow-on effects that influenced the demography of vagrant individuals throughout the landscape, and reduced our ability to differentiate between the different scenarios of recolonisation using demographic signatures.

Although this study was faced with many challenges regarding seasonal confounding, a lack of controls and a high proportion of females, valuable information could still be gathered. Our results suggested that, although forcibly displaced individuals wandering throughout the landscape are an important source of recolonists, most immatures are likely choosing to opportunistically disperse from their original habitat to establish a position within the newly vacant habitat and gain a competitive advantage. However, because their abundance fluctuates with season, they may only be an important source of recolonists following spring. Another source of recolonists was adult individuals, including both subordinate floaters and mature females that had previously held breeding status, inferring they chose to immigrate, individually or within a group, for a competitive advantage. Although the unchanged demography found within the recolonised September population could be due to an effect of the relatively low sex-bias found in the area, it is more likely the result of neighbouring colonies or coteries spreading out and taking advantage of the available habitat before the breeding season. Whether this occurs through the extension of boundaries, or through shifting boundaries, by a colony or coterie, is outside the scope of this study. Regardless, it is clear that Noisy Miner recolonisation can be driven by an influx of colonies/coteries, vagrant individuals, or both, and that multiple factors including season, patch size, patch connectivity, and the sex ratios of nearby colonies, may influence the type of recolonisation that occurs following removal.

Additionally, if landscapes supporting low proportions of females are recolonised differently to landscapes supporting high proportions of females, then sex ratios could have an important influence on the success of culling. If culling within areas of low sex-bias results in similar
demographics amongst recolonists, their effect on resident avifauna will likely remain unchanged, however, if culling within areas of high sex-bias results in very different demographics amongst recolonists, such as the expected higher proportion of females, then recolonists may at least have a reduced capacity to exclude smaller bird species.

Whilst these results are confusing, and confounded, they suggest that the timing of a cull may have a significant effect on whether it is successful or not. Our data suggests that the main source of recolonisation varies with season, based on the availability of individuals within the landscape, and the degree of competition for productive activity spaces. As most breeding occurs during the more productive months of spring (Higgins et al. 2001), culling should be tested temporally; before, during, immediately after, and some months after the height of the spring breeding season. This is necessary, because culling carried out at the wrong time, such as immediately after breeding season, may in fact result in a recolonised population with more Noisy Miners than the population prior to the cull. Determining the effect of season on the outcome of culling holds significant implications for threat abatement, and would greatly assist in developing guidelines for the effective culling of Noisy Miner populations.

Future studies focussed on how culling influences the demography of recolonised populations should eliminate uncertainty by either avoiding the breeding season or implementing the appropriate controls. Sites that support typical male-biased colonies should be selected to allow greater differentiation between the demographic signatures of vagrant individuals and neighbouring colonies. However, subjecting sites with varied sex ratios to culling would assist in evaluating the role that sex ratios play in facilitating different types of recolonisation. An increased understanding of how colonies form, interact, and disperse throughout linear habitats, when compared with large, isolated habitats, would also hold significant implications for the management of the species. Results from such studies may shed light on how the dispersal and spacing behaviour, social systems and sex ratios of Noisy Miners have adapted to modified environments, and how we can effectively mitigate their abundance.
References


McDonald, P. G. & Griffith, S. C. (2012). Feather sampling provides an unreliable source of DNA that may well have significant long-term impacts: A reply to katzen et al. Journal of Avian Biology, 43, 18-20.


Rudd, A. 2016, ‘Maximising despotic potential: Noisy miners (*manorina melanocephala*) exhibit urban wildlife syndrome.’, Bachelor of Science (Advanced)(Honours) thesis, University of Sydney, Sydney NSW.


Appendices

Appendix A.1

Table A.1.1. Comparison between mean measurements from a single recorder and mean measurements from all other recorders. Differences between means were tested for significant using Student’s t-test. All parameters were found to have non-significant differences, except for tail length, which had significantly different means between a single recorder and combined recorders. Means are shown with ± 1SD, and p values are significant if p < 0.0083 after Bonferroni correction. * represents significance of Student’s t-test results.

<table>
<thead>
<tr>
<th>Character</th>
<th>Single recorder</th>
<th>Combined recorders</th>
<th>t-test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean</td>
<td>n</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>448</td>
<td>60.49 ± 5.32</td>
<td>240</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>430</td>
<td>134.14 ± 5.77</td>
<td>241</td>
</tr>
<tr>
<td>Total head length (mm)</td>
<td>442</td>
<td>47.39 ± 1.47</td>
<td>229</td>
</tr>
<tr>
<td>Tail (mm)</td>
<td>159</td>
<td>120.70 ± 5.26</td>
<td>238</td>
</tr>
<tr>
<td>Culmen (mm)</td>
<td>155</td>
<td>18.82 ± 1.40</td>
<td>231</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>158</td>
<td>30.67 ± 1.27</td>
<td>235</td>
</tr>
</tbody>
</table>

Table A.1.2. The number of individual Noisy Miners used from each of six recorders (#1-#6) in producing the mean measurements presented in Table A.1.1.

<table>
<thead>
<tr>
<th>Recorders</th>
<th>#1</th>
<th>#2</th>
<th>#3</th>
<th>#4</th>
<th>#5</th>
<th>#6</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combined</td>
<td>0</td>
<td>58</td>
<td>56</td>
<td>51</td>
<td>43</td>
<td>38</td>
<td>246</td>
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<tr>
<td>Single</td>
<td>459</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>459</td>
</tr>
</tbody>
</table>

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### Appendix A.2

**Table A.2.1.** The number of individual Noisy Miners used from each of six recorders (#1–#6) for the initial stepwise discriminant analysis and the following discriminant function analyses, which only used head length and wing length as parameters. Cases with missing values relevant to the function were omitted from analysis.

<table>
<thead>
<tr>
<th>Recorder</th>
<th>#1</th>
<th>#2</th>
<th>#3</th>
<th>#4</th>
<th>#5</th>
<th>#6</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Step-wise discriminant analysis</td>
<td>159</td>
<td>58</td>
<td>56</td>
<td>51</td>
<td>43</td>
<td>38</td>
<td>405</td>
</tr>
<tr>
<td>Discriminant function analyses ($C_1, C_2, ...$)</td>
<td>459</td>
<td>58</td>
<td>56</td>
<td>51</td>
<td>43</td>
<td>38</td>
<td>705</td>
</tr>
</tbody>
</table>

### Appendix A.3

**Table A.3.1.** Discriminant function analyses including between one and five variables, the best sets variables are used as determined by “stepping backwards” from five variables to one. Wing and head length are, in combination, the best predictors of sex. $C_1$ and $C_2$ denote the parameters used and their associated values for the equations seen in Results.

<table>
<thead>
<tr>
<th>Variables used in analysis</th>
<th>Wilks Eigenvalues</th>
<th>SCC Lambda F df p</th>
<th>Discrimination rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing, Head, Tarsus, Tail,</td>
<td>1.12 0.53 0.47 273.7 5, 366 &lt;0.001</td>
<td>88.0%</td>
<td></td>
</tr>
<tr>
<td>Culmen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wing, Head, Tarsus, Tail</td>
<td>1.11 0.53 0.47 272.5 4, 367 &lt;0.001</td>
<td>87.3%</td>
<td></td>
</tr>
<tr>
<td>Wing, Head, Tarsus</td>
<td>1.10 0.52 0.48 274.2 3, 372 &lt;0.001</td>
<td>88.0%</td>
<td></td>
</tr>
<tr>
<td>Wing, Head (C_1)</td>
<td>1.29 0.56 0.44 535.8 2, 648 &lt;0.001</td>
<td>90.0%</td>
<td></td>
</tr>
<tr>
<td>Wing (C_2)</td>
<td>0.94 0.48 0.52 442.3 1, 669 &lt;0.001</td>
<td>85.1%</td>
<td></td>
</tr>
</tbody>
</table>
Appendix B.1

**Table B.1.** Total Noisy Miners shot in each of the six sites for each of the three removals during Davitt’s (2016) study, and the associated area (ha) for each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Aug-15</th>
<th>Sep-15</th>
<th>Apr-16</th>
<th>Total</th>
<th>Area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C08</td>
<td>77</td>
<td>49</td>
<td>110</td>
<td>236</td>
<td>32</td>
</tr>
<tr>
<td>C32</td>
<td>55</td>
<td>35</td>
<td>98</td>
<td>188</td>
<td>32</td>
</tr>
<tr>
<td>C35</td>
<td>62</td>
<td>77</td>
<td>143</td>
<td>282</td>
<td>49</td>
</tr>
<tr>
<td>C42</td>
<td>67</td>
<td>60</td>
<td>145</td>
<td>272</td>
<td>37</td>
</tr>
<tr>
<td>C45</td>
<td>33</td>
<td>23</td>
<td>21</td>
<td>77</td>
<td>36</td>
</tr>
<tr>
<td>C52</td>
<td>45</td>
<td>38</td>
<td>74</td>
<td>157</td>
<td>16</td>
</tr>
<tr>
<td>Total</td>
<td>339</td>
<td>282</td>
<td>591</td>
<td>1212</td>
<td>202</td>
</tr>
<tr>
<td>Mean Density (Birds/ha)</td>
<td>1.82</td>
<td>1.47</td>
<td>3.09</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>