Declining small woodland birds: is removing noisy miners the answer?

by

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Candidate's Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author's knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Richard Bezgy July 2020

Preface

This thesis is a Thesis by Compilation and conforms to the requirements of the procedure for Higher degree by research - thesis by compilation and thesis by creative works of the Australian National University (https://policies.anu.edu.au/ ppl/document/ANUP_003405). The thesis is presented as a series of four papers that have been published, are under review, or will be submitted to peer review journals. Each paper is a stand alone work and the relevance of each to the overall project is summarised in a foreword at the start of each chapter. The text of published papers has not been changed but some changes in formatting have been made to ensure consistency throughout the thesis. Remaining differences in style or format reflect different journal requirements. The thesis begins with an extended introduction to provide an understanding of the background to the work and to explain the connection between the four papers. Whilst I did the majority of the work behind the thesis, the first three papers were written with the collaboration of other authors. Each paper begins with a Statement of Contribution listing author contributions and the status of the paper with regard to publishing. The content of each Statement of Contribution has been agreed by all co-authors.

Acknowledgements

When I set out on this project in 2015, I was looking for a further intellectual challenge to follow the one represented by the MSc in Environmental Management that I completed at the University of Western Australia in 2014. I soon came to realise that the intellectual element is only one part of the PhD process. The other is the tremendous psychological challenge of working mostly alone with little productive output initially and doing things way beyond one's comfort zone. Someone once said that doing things you are good at is an essential ingredient of happiness. For most of the first two years of my PhD I was daily reminded of what I was not good at. In spite of frequent pledges to myself to just give up and walk away, early in the process I resolved that I would keep going, step by step and day by day. At the same time, I resolved not to sacrifice my physical or mental health for the purpose of achieving a mere academic credential. Maintaining my physical health was up to me, but an important component of the maintenance of my mental and emotional health was the support I received from other people. These people were friends, family, academic staff and admin staff. In particular, I thank my supervisors, David Lindenmayer, Jenny Pierson and Ayesha Tulloch, for finding the right balance between pressure and support. Among my other co-authors, Wade Blanchard's statistical counsel was only bettered by his patience in trying to convey it to a novice like me; Mason Crane's knowledge and experience of the study region was essential for the success of the project; and Martin Westgate brought a useful combined understanding of ecology and modelling to the project. Amongst my friends I was fortunate to count (in no particular order) Mishka Talent, Carl Tidemann, Alex Van der Meer Simo, Claudia Munera, Peter Ramshaw, Micah Wood, Linda Iaccheri, Tom North, Serrin Rutledge-Prior, Ted Fingleton-Smith, Miriam Potter, Vicky Shukuroglou, Catherine Ross, Elle Bowd, James Latimer, Donna Belder, Szabina Horvath, Marie-France Duhamel and Yuan Peng.

My parents deserve mention for their role in my early intellectual development and for instilling in me a natural curiosity about the world. The more I hear about the dysfunctional upbringing of other people, the more I realise how lucky I was (and am). During a sojourn in rural Devon in 1972, when I was six, my mother sat with me before the school bus arrived and, with the help of the Ladybird Book of Garden Birds, we identified the visitors to our bird table. Always good at supporting any display of interest, later that year my father gave me as a Christmas present an annual subscription to the Young Ornithologist's Club of the Royal Society for the Protection of Birds. So began a lifelong love and appreciation of the natural world.

Finally, I wish to acknowledge my father's generosity in providing subsidised accommodation during this period of study. This support meant that I was able to devote myself to my studies without the burden of having to earn income additional to my scholarship. Without it, the whole undertaking would have been even more onerous than it already was.

Abstract

Overabundant native species are a growing problem globally, in large part due to anthropogenic landscape modification. They are organisms whose abundance exceeds the carrying capacity of a given social-ecological system. The carrying capacity may be ecological or cultural. The cultural carrying capacity is the upper population density of an overabundant species accepted by human society due to non-ecological impacts such as nuisance or disease risk. Native organisms that exceed a cultural or ecological carrying capacity may require management interventions to reset ecological or cultural equilibrium. An overabundant native species with major ecological impacts in Australia is the noisy miner, Manorina melanocephala, an endemic, sedentary, colonial species with a preference for fragmented woodland landscapes. Noisy miners aggressively exclude all smaller woodland birds from colonized territory. Many small woodland birds are in serious decline due to habitat loss and noisy miners are an additional threat that could drive some to extinction. Noisy miners now dominate remnant woodland in eastern Australia at a sub-continental scale. In 2014 their aggressive behaviour was listed as a Key Threatening Process under federal conservation legislation. Some ecologists recommend culling as the best management option to prevent further declines of small woodland birds. Evidence that culling noisy miners benefits small woodland birds is limited.

To assess the feasibility of culling as a management intervention applicable at a broad scale to improve ecosystem function, I conducted a controlled and costed experimental cull of noisy miners in woodland patches in an agricultural landscape of south east Australia. I monitored foraging and harassment rates of small woodland birds before and after the cull. The purpose here was fourfold: to assess the amount of harassment carried out by noisy miners; to see if small woodland birds suffered less overall harassment after the cull; to indicate if there was any compensatory harassment by other aggressive species; and to see if removing noisy miners improved foraging opportunities for small woodland birds.

Successful breeding is essential for recovery of declining species. I therefore assessed post-cull changes in breeding potential of small woodland birds. In this landscape, nest predation is the principal cause of breeding failure and birds are the principal nest predators. Small woodland birds make few breeding attempts in sites colonized by noisy miners, however, due to aggressive disruption of nesting by noisy miners. I therefore conducted pre- and post-cull artificial nest predation experiments. I aimed to show the proportion of nest predation carried out by noisy miners and to indicate any compensatory nest predatory responses by other species.

My principal finding was the unexpected immediate recolonisation of treatment sites by noisy miners. Although noisy miner abundance in treatment sites post-cull was 25% lower than in control sites, abundance in all sites remained three to four times higher than ecological impact thresholds. Nonetheless, the cull disrupted intraspecific relations of this socially complex species, so I expected some effect on the responses of small woodland birds. Foraging rates doubled but I recorded no change in harassment rates. In my nest predation study, noisy miners were responsible for 18% of nest predation events where the predator was identified. I recorded predation by five other bird species but I detected no significant change in artificial nest predation rates post-cull. I conclude that in highly modified agricultural landscapes such as this, patch-scale culling is not an effective management option due to rapid recolonisation.

A second element of this thesis is a cultural history of the noisy miner. Through exploration of historical references I chart the shift in cultural attitudes to the species in parallel with its changed ecological role. As an antidote to environmental amnesia, this chapter provides an understanding of the social-ecological changes that have occurred in south east Australia since European settlement. These changes have fostered the transformation of a natural ecosystem process, interspecific competition, into a Key Threatening Process.

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Chapter 1: Introduction and Synthesis

1.1 Introduction

1.1.1 Foreword: when natural ecosystem processes become threatening processes

Overabundant native species are a growing problem globally, often as a result of anthropogenic landscape modification (Garrott *et al.*, 1993; Mendelssohn and Yom-Tov, 1999; Livezey, 2010). The term "overabundant species" is used in contrast to "invasive species," the latter used to refer to species that have changed their distribution and generally applied to exotic species. Overabundant species are native organisms whose otherwise normal ecological activities, such as foraging, predation, competition and brood parasitism, exceed the carrying capacity of a given social-ecological system. The carrying capacity may be ecological (Caughley, 1981) or cultural (Ellingwood and Spignesi, 1986; Dubois *et al.*, 2017). The cultural carrying capacity is the upper limit of population density of an overabundant species accepted by human society due to non-ecological impacts such as nuisance effects. Native organisms that exceed a cultural or ecological carrying capacity may require management interventions to reset ecological or cultural equilibrium.

Overabundant species are an ecological issue in multiple locations and across taxa, frequently occurring as a result of anthropogenic disturbance to ecosystems. Particularly significant disturbances include removal of predators, habitat modification, and interactions between the two. Declines in populations of the wolf (Canis lupus) in North America due to persecution mean that populations of herbivorous prey species such as white-tailed deer (Odocoileus virginianus), elk (Cervus elaphus) and moose (Alces alces) have burgeoned, with consequent impacts on desired states of native vegetation (Nugent et al., 2011). Similar problems have been observed in eastern Australia where control of the introduced red fox (Vulpes vulpes) has led to overabundance of herbivorous prey species such as the swamp wallaby (Wallabia bicolor) (Dexter et al., 2013). Declines in apex predators due to culling or habitat fragmentation can precipitate an overabundance of mesopredators with consequent declines in mesopredator prey species (Crooks and Soulé, 1999; Eagan et al., 2011). Examples include overabundance of coyotes (Canis latrans) in North America due to reduced interference competition from wolves (Berger and Gese, 2007). Such changes in species assemblages can precipitate trophic cascades, with consequent phase shifts in ecosystem function (Crooks and Soulé, 1999; Ripple et al., 2001)). Landscape modification due to agricultural development may favour some species to the extent that they become overabundant. The brood parasitic brown-headed cowbird (*Molothrus ater*) has benefitted from agricultural development in North America (Rothstein and Peer, 2005). Host species that are disadvantaged by such landuse change may then suffer further declines due to increased brood parasitism from cowbirds. Landuse change in Southern Africa has caused local overabundance of elephants (*Loxodonta Africana*) through compression of populations into limited areas, leading to ecological and economic impacts (Balfour *et al.*, 2007). Food subsidies provided by agricultural crops may increase winter survival in some species, causing overabundance and economic or ecological impacts eg red-winged blackbird (*Agelaius phoeniceus*) (Dolbeer, 1990) and lesser snow geese (*Chen caerulescens caerulescens*) (Abraham *et al.*, 2005) in North America. The replacement of native vegetation with grazing land for domestic stock in arid areas may result in overabundance of native herbivores through water and food subsidies (Coulson, 1998).

An overabundant species with a major ecological impact in Australia is the noisy miner, Manorina melanocephala (Dow, 1977; Thomson et al., 2015). Endemic to eastern Australia, the noisy miner is a native woodland bird of the honeyeater family, Meliphagidae. Many genera in this family display aggressive interference competition but most act individually, seasonally and at a scale localized to individual food resources such as a tree or inflorescence (Ford and Paton, 1976; Ford, 1979; Ford, 1989). The noisy miner, in contrast, is a sedentary species that permanently colonises whole patches of woodland and defends them co-operatively (Dow, 1977). It is a medium-sized honeyeater with a weight of 70 - 80g (Higgins et al., 2001). At densities as low as 0.6 individuals/ha, the noisy miner aggressively excludes all woodland birds smaller than itself (and some larger) from woodland (Thomson et al., 2015). Many small nectarivorous and insectivorous woodland birds are already in serious decline due to habitat loss (Higgins et al., 2001; Paton and O'Connor, 2009; Ford, 2011a). Noisy miners represent an additional threat that may drive some small woodland birds to extinction (Ford, 2011b; Maron et al., 2013). Noisy miners have been described as a reverse keystone species, their presence having negative ecological impacts disproportionate to their biomass (Piper and Catterall, 2003; Montague-Drake et al., 2011). As a reverse keystone species, noisy miners play a critical role in structuring avian assemblages and are associated with larger generalist and granivorous species (Montague-Drake et al., 2011; Thomson et al., 2015). Noisy miners now dominate remnant woodland in eastern Australia at a scale of more than a million km² (Mac Nally et al., 2012). In 2014 aggressive exclusion of woodland birds from potential habitat by noisy miners was listed as a Key Threatening Process under the federal 1999 Environment Protection and Biodiversity Conservation Act (Department of the Environment, 2014). This is the first case in Australia of a natural ecosystem process, in this case interference competition, exerted by a native species being listed federally as a threatening process.

As a native species, the noisy miner has been co-evolving with Australian ecosystems for millions of years. The transformation of its successful competitive behaviour into a threatening process was first recorded in the 1970s and is linked to two centuries of landscape modification following the European invasion of the continent (Dow, 1977; Mac Nally et al., 2012). Noisy miners have a preference for small patches of open eucalypt woodland with minimal understorey (Maron et al., 2013). Such habitat provides for all their breeding and foraging needs and ensures efficient detection and eviction of competitive intruders (Maron et al., 2013). Fragmented open woodland is now common across eastern Australia, particularly in the sheep-wheat belt that lies inland of the Great Dividing Range. Here, clearing of eucalypt woodland for agriculture and continued grazing of remnant woodland fragments, preventing development of a shrub layer, has ensured the perfect configuration of vegetation for noisy miners at both patch and landscape scale. This same configuration has contributed to declines in small woodland birds, which require more complex vegetation structure for foraging, breeding and refuge from aggressive species (Ford et al., 2001).

Whilst the principal focus of this thesis is management of the noisy miner, the underlying theme is the decline in small woodland birds in eastern Australia. The judgement of people, including conservation biologists, can be influenced by their personal feelings, positive or negative, about particular species (Cox and Gaston, 2015; Lambert, 2016; Nelson *et al.*, 2016). Invasive or overabundant species often rouse the most negative feelings (Lambert, 2016; Lidström *et al.*, 2016; Duncan, 2018). The degree to which such feelings influence the choice of management response is open to debate (Lidström *et al.*, 2016). Notwithstanding such personal or cultural antipathy towards particular species, elimination of overabundant or invasive species is rarely an end in itself. The purpose of management of invasive or overabundant species such as the noisy miner is the protection of other species or communities threatened by them.

Noisy miners represent a severe threat to small woodland birds in eastern Australia, but they are only one threat among many (Paton and O'Connor, 2009; Ford, 2011a). Because of the critical role of anthropogenic habitat modification in the evolution of the noisy miner threat, a full understanding of the ecological impacts of noisy miner overabundance is impossible without consideration of the broader ecological effects of habitat modification since the European invasion of the continent. I begin this introduction, therefore, with an account of how Australia's extremely rapid habitat modification may have directly affected the abundance and distribution of small woodland birds (section 1.1.2).

All four of Australia's endemic *Manorina* species use aggressive interference competition in co-operative defence of territory, making them particularly successful in monopolising resources (Mac Nally *et al.*, 2014). Interference competition is common among Australian avifauna, however, particularly within the family *Meliphagidae* (Ford and Paton, 1976; Ford, 1989; Chan, 2004). This is the result of a number of biophysical characteristics unique to Australian ecosystems (Orians and Milewski, 2007). Given the importance of interference competition in woodland assemblages, I explore the ecological role of competition in sections 1.1.3 and 1.1.4. I then consider how the particularly extreme manifestation of interference competition practised by noisy miners represents a "threat multiplier" to small woodland birds already affected by landscape transformation.

The federal listing of noisy miner aggression as a Key Threatening Process made management of the threat a legal obligation. The listing made no overall management recommendation, however, referring instead to revegetation and/or lethal control as possible interventions according to local conditions. There is evidence that well-designed ecological restoration can both deter noisy miners and support declining small woodland birds (Hastings and Beattie, 2006; Clarke and Grey, 2010; Tulloch *et al.*, 2016b; Lindenmayer *et al.*, 2018). However, a number of culls and translocations of noisy miners have been conducted in the last three decades, with varying levels of success (Grey *et al.*, 1997; Grey *et al.*, 1998; Debus, 2008; Davitt *et al.*, 2018). In section 1.1.5 I discuss the options for managing noisy miner populations and report on current knowledge of the efficacy of noisy miner aggression. Acknowledging the context of the wider social-ecological system within which the noisy miner problem has evolved, this section also defines the bounds of this study.

Section 1.1.6 presents the aims of the study, as well as a brief description of the study region. I follow this with a summary of principal outcomes, finishing this introductory chapter with a synthesis of the different elements of the study and a conclusion. The synthesis considers the significance of the outcomes of the study and how the outcomes integrate into the broader question of management of overabundant and invasive species. The section also explores some of the limitations of the study and suggests possible solutions.

1.1.2 The multiple threats to small woodland birds: Landscape transformation and biodiversity loss in the Anthropocene

Populations of many wild birds are in decline globally due to loss of habitat associated with human development (Butchart *et al.*, 2010). With global human population expected to exceed 9 billion by 2050 (UN Department of Economic and Social Affairs Population Division, 2015) this decline is likely to continue under the pressure to increase agricultural production. The ecological consequences are likely to be significant as agriculture intensifies, and remaining areas of native vegetation undergo further disturbance. Climate change represents a further threat to birds through its impact on vegetation, associated spatial changes in resource availability, and influence on multiple ecosystem processes (Bennett *et al.*, 2009; Mac Nally *et al.*, 2009).

Australia is not immune to the global problems outlined above, with a continuing annual net loss of native vegetation and an assumption at policy level that agricultural productivity must rise in response to growing global food demand (Paton and O'Connor, 2009; Australian Government, 2015). Small woodland birds are among the most threatened of any avian group, with many species in chronic decline across the eastern states and a number now threatened, endangered or critically endangered (Ford *et al.*, 2001; Paton and O'Connor, 2009) (but see Rayner *et al.*, 2014).

1.1.2.1 Habitat loss

The decline in woodland birds is primarily a result of the broadscale loss, fragmentation and degradation of native woodlands for agricultural development since European settlement (Lindenmayer *et al.*, 2010a). Eucalypt woodland in the south-east and the south-west of the country has been preferentially cleared as it tends to occupy the most productive land (Hobbs and Hopkins, 1990; Robinson and Traill, 1996; Beresford, 2001). Eighty-five per cent of the original extent of southern temperate woodlands has been cleared, with local rates of loss often higher (Olsen *et al.*, 2005; Benson, 2008).

Depending on the metric in question, habitat loss or invasive species are the principal threats to Australian biodiversity (Evans *et al.*, 2011; Kearney *et al.*, 2018). Habitat loss is listed in the national Biodiversity Conservation Strategy 2010-2030 as the main threat to Australian ecosystem resilience (Australian Government Department of the Environment, 2016). The process of clearing native vegetation, principally for agriculture, increased during the post-war economic boom known as the "Great Acceleration" (Steffen *et al.*, 2015). Fifty per cent of all clearing for

agriculture has happened since the 1970s whilst between 1990 and 2000, Australia was sixth globally in rate of land clearing and the only developed nation in the top 20 (Lindenmayer, 2007). Broadscale deforestation continues and the nation may consequently be incapable of meeting its international obligations to maintain biodiversity (Paton and O'Connor, 2009; Evans, 2016). More recently the nation was declared a global deforestation hotspot (WWF, 2015). Loss of habitat causes declines in bird populations proportionate with the extent of clearing until losses approach 70% when crashes may occur (Connor and McCoy, 1979; Woinarski *et al.*, 2006). Along with direct loss of habitat, fragmentation and degradation of remaining habitat impact biodiversity in various ways.

1.1.2.2 Habitat Fragmentation

At levels of remnant woodland below 20-30%, fragmentation has a disproportionate impact on wildlife populations (Ford *et al.*, 2009). Because of their relatively large edge, isolated fragments are more vulnerable to disturbance such as grazing, fire and invasive species. This vulnerability in turn makes them more likely to become degraded or suffer changes in vegetation structure, with a consequent decline in resource availability (Saunders *et al.*, 1991; Fischer and Lindenmayer, 2007).

Fragmentation implies a loss of connectivity which imposes dispersal costs on birds (Saunders *et al.*, 1991; Ford *et al.*, 2001). In addition, the lag between loss and fragmentation of habitat and full expression of the ecological impacts means that in many cases an extinction debt remains to be paid (Tilman *et al.*, 1994; Ford, 2011b). This lag may be particularly long in Australia where many birds have longer lifespans than elsewhere in the world (Ford *et al.*, 2001). Small, isolated metapopulations are less viable and may decline over time faster than new patches are colonised, sometimes finally going extinct years after the original habitat modification (Ford, 2011b).

In general, larger areas of habitat support greater biodiversity (Connor and McCoy, 1979). This species-area relationship has also been shown to be true in relation to woodland patch size in fragmented landscapes with smaller patches supporting fewer species (Fischer and Lindenmayer, 2002b; Chan, 2004). Whilst patches of less than 5-10ha may be ecologically unviable in the long term (Freudenberger, 1999; McIntyre *et al.*, 2004), small patches would ordinarily represent a complement to conservation of larger areas (Margules and Pressey, 2000). In highly cleared and fragmented landscapes, such as the intensively cultivated areas of south east and south west Australia, however, there is little in the way of conservation tenures to complement. Small patches typically represent the

bulk of remaining native vegetation and, in spite of their vulnerability, are therefore potentially even more important as contributors to overall biodiversity (Fischer and Lindenmayer, 2002; Tulloch *et al.*, 2016a; Lindenmayer, 2019).

1.1.2.3 Habitat degradation

Much of the open woodland of inland south east Australia would have consisted of a discontinuous overstorey of eucalypts with clearly separated canopies, a midstorey of scattered shrubs and a species-rich understorey of native tussock grasses and forbs interspersed with coarse woody debris (Department of Environment Climate Change and Water, 2010). The multiple components of such structure represent habitat for a wide range of foraging guilds as well as offering a variety of nesting opportunities. Conversely, loss of any part of this structure will reduce diversity of birds through its impacts on the respective foraging guild and in reducing nesting opportunities (Ford *et al.*, 2001).

Remnant fragments of native woodland have been severely impacted by the grazing, exotic grasses, invasive weeds, and altered fire regimes that have accompanied the development of European-style agricultural systems (Hobbs and Hopkins, 1990). Grazing by cattle and sheep is the single biggest land use in Australia (Australian Collaborative Land Use and Management Program, 2011). Intensive grazing is associated with soil erosion and compaction, changed hydrological and nutrient regimes, loss of litter, altered composition of ground layer, tree damage and constrained recruitment of shrubs and trees, all of which affect small woodland birds (Hobbs and Hopkins, 1990; Martin and McIntyre, 2007; Tulloch *et al.*, 2016b). Watson (2011) posits a productivity-based explanation for the declines in insectivores. Through their impact on soil saprophytes, changes in water and nutrient cycles have affected woodland food webs at all trophic levels, with fewer ground-dwelling invertebrates and consequently fewer insectivores.

1.1.3 Habitat modification: novel ecosystems, changes in interspecific competition and new avian assemblages

Anthropogenic habitat modification across agricultural landscapes of eastern Australia has disrupted multiple ecosystem processes. This disruption has led to a loss of ecosystem resilience, an increased chance of local extinctions and the creation of novel ecosystems with changed species assemblages, (Ford *et al.*, 2001; Lindenmayer *et al.*, 2008). Interactions between habitat change, resource depletion and interspecific competition benefit some species whilst disadvantaging others. Small woodland birds are the principal losers from such changes in ecosystems, whilst larger generalist species such as pied butcherbirds (*Cracticus torquata*), magpies (*Cracticus tibicen*), currawongs (*Strepera spp*) and corvids (*Corvus spp*) have been winners (Montague-Drake *et al.*, 2011; Mac Nally *et al.*, 2012; Maron *et al.*, 2013). These aggressive and nest-predatory species are able to cross the boundary into the edge of woodland from the surrounding agricultural matrix and their presence further reduces reproductive success of many small nectarivores and insectivores (Grey *et al.*, 1998; Zanette and Jenkins, 2000; Fischer and Lindenmayer, 2002; Rayner *et al.*, 2014; Robertson *et al.*, 2014). Foremost among the beneficiaries of habitat change, however, is the noisy miner.

1.1.3.1 Habitat preferences: how habitat modification suits noisy miners

High noisy miner densities are associated with woodland fragments that are productive, colonisable and defendable (Maron et al., 2013). Small (<300ha) patches of open eucalypt woodland with a high perimeter to area ratio and minimal understorey fulfil all these requirements. The impacts of noisy miners are greatest in small fragments where there is no core of vegetation accessible to smaller birds (Loyn, 1987; Ford et al., 2001). The species has a preference for woodland or forest edges, possibly because of greater productivity (Oldland et al., 2009; Thomson et al., 2015). Any patch with a width/diameter of less than 600m may be considered all edge since noisy miners will penetrate up to 300m into patches depending on density of vegetation structure (Clarke and Oldland, 2007). In agricultural landscapes they will move out from edges to forage in the open country of the matrix between woodland patches (Grey et al., 2011). Open woodland with minimum understorey ensures good visibility and efficient defence (Grey et al., 2011; Montague-Drake et al., 2011). Hence, grazing of woodland patches in agricultural landscapes fosters noisy miner colonisation (Grey et al., 2011; Tulloch et al., 2016b). Changes at both landscape and patch scale due to clearing for agriculture and grazing of remnant fragments have created a large area of eastern Australia ideally suited to colonisation by noisy miners. The species is now dominant at a sub-continental scale (Mac Nally et al., 2012). The consequence has been that interspecific competition, ordinarily a natural ecosystem process, has become a threatening process for many small woodland birds vulnerable to noisy miner aggression (Department of the Environment, 2014).

Aggressive interference competition is a common phenomenon amongst Australian birds (Low, 2014). Some ecologists, however, consider the impact of noisy miner aggression on species assemblages to be unique globally (Dow, 1977; Maron *et al.*, 2013) because of the combination of a sedentary habit, co-operative defence of territory, and highly intense and persistent aggression. Co-operative aggression has been recorded in other bird species, such as fieldfare (*Turdus pilaris*) and red-winged blackbirds (*Agelaius phoeniceus*), but it is rare and confined to nest defence rather than resource competition (Meilvang *et al.*, 1997; Weatherhead and Sommerer, 2001). In the following section I consider in greater detail the role of competition in woodland bird assemblages and highlight the particular characteristics of the noisy miner which make its impacts so severe.

1.1.4 The ecology of exclusion: defendable resources, interference competition and the special case of noisy miners

The modification of landscapes in eastern Australia since European settlement has had a major ecological impact on many woodland birds through changes in mortality, breeding success, dispersal and species assemblages (Mac Nally and Bennett, 1997). Krebs (1972) notes that after geo-physical barriers to movement, interspecific interactions such as predation, brood parasitism and competition for resources make up the next most important influence on distribution of birds. These ecological processes exert a significant effect on ecosystem function through their influence on relative abundance, fecundity and survival of individuals of different species (Ewers and Didham, 2006). The long term, evolutionary effect of competition is that species change to improve their competitive position with respect to other species. The ecological effect, which may manifest in the much shorter term, is a change in the relative abundance of different species in a particular habitat.

Interactions between ecologically similar species may permit or prevent coexistence. Indeed, competitive pressure has facilitated the evolution of specialisation in, for example, foraging habits. Different species may use the same substrate in different ways or may adapt to use of different substrates (Heppleston, 1972). In rich areas of eucalypt woodland, for example, 10 or more species of honeyeater may occur along with other nectarivores such as silvereyes (*Zosterops lateralis*) and lorikeets (*Trichoglossus* spp.) (Ford, 1979). Coexistence is facilitated by the different nutritional balance between insects and nectar displayed by the different species. Shorter-billed genera such as *Meliphaga, Manorina, Lichenostomus* and *Melithreptus* will take relatively more insects and non-nectar plant carbohydrate such as lerp, manna and honeydew. The diet of the noisy miner, for example, consists of 75% insects and 25% plant sugars (Higgins *et al.*, 2001). Longer-billed genera, on the other hand, such as *Phylidonyris, Acanthorhynchus* and *Antochaera*, are more dependent on nectar. Different genera show further specialisation in terms of preferred flowers (Ford, 1989).

Interspecific competition where all species gain some access to resources and those resources are used until depleted is termed exploitation competition (Tilman, 1982). In contrast, interference competition implies monopolisation of defendable resources by one group through aggressive exclusion of competitors (Brian, 1956). The effect is a decline in abundance, survival and reproductive potential in the excluded species. Interference competitors may become "strong interactors," species whose absence would have a major ecological effect (MacArthur, 1972). The ecological effect here may be a change not just in relative abundance of different species, as with exploitation competition, but a permanent change in species assemblage.

The traditional (i.e. Northern Hemisphere) view was that in most stable ecosystems, birds interact peaceably through exploitation competition, with different species using resources in slightly different ways and avoiding conflict (Low, 2014). Outside Australia, there are only a few examples of strong interactors among avifauna (Dow, 1977). South American cotingas cooperate in defence of group territories against predatory birds (Snow, 1971); the Californian acorn woodpecker practises aggressive, co-operative defence of food resources against conspecifics and any other species which approaches their store of acorns in tree hollows (MacRoberts, 1970). In Australia, however, such strong interactors are common amongst birds. Whilst coexistence through exploitation competition for nectar occurs between smaller Australian honeyeaters, larger honeyeaters tend to dominate the richer and more reliable trees or flowers through interference competition, pushing smaller, less competitive nectarivores to poorer areas (Ford and Paton, 1976; Ford, 1979; Mac Nally et al., 2005). Hence, whilst the competitive aggression of all four Manorina species is notorious (Mac Nally et al., 2014), numerous other honeyeaters aggressively defend concentrations of nectar. Gould (1865) described the now critically-endangered Regent honeyeater (Anthochaera phrygia) as "the most pugnacious bird I ever saw."

The temporal and spatial extent of interference competition is a function of resource dispersion spatially and temporally. Resource dispersion is an indication of how economically defendable the resource is (Brown, 1964) and is thus limited by the density and duration of the resource. The degree of resource monopolisation ultimately achieved is determined by a combination of resource dispersion and the extent to which the aggressive species is able to physically exclude competitor species (Emlen and Oring, 1977; Weir and Grant, 2004). These two processes interact in Australia in the form of defendable concentrations of plant carbohydrate vigorously defended by numerous species (Low, 2014).

Australia's plants, particularly the *Myrtaceae* and *Proteaceae*, produce large quantities of expendable carbohydrate in the form of sugars such as nectar, lerps, manna and honeydew. The production of large quantities of nectar ensures

successful pollination and in certain environments has facilitated evolution of large nectarivores that are behaviourally dominant over insectivores (Orians and Milewski, 2007). Consequently, many of Australia's honeyeaters, with access to abundant calories (although not necessarily protein), are larger than nectarivores elsewhere and can become sufficiently locally abundant to limit populations of insectivores through aggression and resource depression. Nectarivores on all continents will attempt to aggressively defend flowers, hummingbirds (family *Trochilidae*) being very aggressive, for example (Ewald, 1985). Outside Australia, however, nectarivorous species are generally too small to dominate the insectivorous birds that share their habitats (Low, 2014).

Body size is an important determinant of the extent to which aggressive species are able to exclude other species from nectar. Larger honeyeaters can expel insectivorous birds from their territories, the aggressive blue–faced honeyeater, for example, being associated with reduced species richness (Chan, 2004; Mac Nally *et al.*, 2005). Competition between honeyeaters can be fierce, with the distribution of the large and morphologically similar genus *Lichenostomus* believed to be largely determined by competition (Ford and Paton, 1976). The aggressively dominant honeyeater, the red wattlebird (*Anthochaera curunculata*), chooses the best sites in terms of flowering intensity. Fewer *Lichenostomus* and *Melithreptus* honeyeaters are therefore found on rich sites, instead being relegated to areas of moderate flowering intensity

For assemblages of honeyeaters, habitat quality in terms of flowering intensity varies both temporally and spatially. Isoleg theory, which attempts to represent spatially the complex combinations of species and habitats in a landscape or patch, has been used to explain the partition of habitat between competitive species. Mac Nally et al (2005) suggest that there is an additional need to capture variation in the spatial extent of habitat of different quality to explain the usefulness of aggression as an adaptation to resource competition. For noisy miners, modelling of presence/absence data in relation to vegetation characteristics has gone some way towards explaining noisy miner occupancy of woodland patches and agricultural landscapes (Mac Nally *et al.*, 2012; Maron *et al.*, 2013; Haythorpe *et al.*, 2014).

In summary, whilst competitive aggression is a common feature of Australian woodland birds, particularly honeyeaters, such aggression is usually solitary and is limited in time and space: individual honeyeaters will defend a tree or flower during nectar production. In contrast *Manorina* species defend large, colonial territories permanently and co-operatively. In modified landscapes, where resource availability is already severely constrained, these particular characteristics transform the natural ecosystem process of interference competition into a threatening process. Further,

these characteristics mean that body size is not the principal determinant of the success of interference competition by *Manorina* species as it is with other honeyeaters.

1.1.4.1 Hyperaggressive, sedentary and co-operative: the unique characteristics of noisy miners

Aggressive exclusion of smaller woodland birds by noisy miners in modified landscapes is a particularly extreme manifestation of a natural Australian tendency towards interference competition. The permanent, colonial territoriality of noisy miners in fragmented woodland, combined with extreme aggression, has been implicated in the chronic decline of a wide range of smaller woodland birds, especially nectarivores & insectivores (Dow, 1977; Grey *et al.*, 1998; Ford *et al.*, 2001; Grey *et al.*, 2011; Mac Nally *et al.*, 2012; Maron *et al.*, 2013; Howes *et al.*, 2014). Noisy miner aggression represents a barrier to distribution, further limiting the availability of resources to woodland birds already suffering the impacts of habitat loss and fragmentation. The particular behavioural characteristics of the noisy miner interact with anthropogenic habitat modification to create a domination of woodland fragments at a sub-continental scale.

Among woodland birds, the noisy miner is a medium-sized bird, 24-28cm in length and weighing 70-80g (Higgins *et al.*, 2001). Aggressive dominance in passerines is a function of weight (Ford, 1979; Mac Nally *et al.*, 2005). The size advantage of noisy miners allows them to aggressively exclude almost all smaller woodland passerines. Co-operative defence of territory means noisy miners will also aggressively interact with larger animals. They have been recorded harassing 65 bird species, including such non-competitive taxa as waterbirds, but will also harass many other vertebrates (Dow, 1970; Dow, 1977). Intensity of harassment ranges from simple alarm calls through to physical attack and fatal injuries.

Like all *Manorina* species, noisy miners have complex intraspecific social relations at family, coterie and colonial levels. Males outnumber females in colonies by more than 3:1 and they breed communally. Whilst the species is predominantly monogamous (Põldmaa and Holder, 1997), a family group, or coterie, of several males and juveniles will support one breeding pair, feeding young both in the nest and after they have fledged (Dow, 1978; Higgins *et al.*, 2001). The nest is constructed by the female amongst foliage in eucalypts or other trees (Dow, 1978). Clutch size is two to four, incubated only by the female and incubation takes 16 days but is asynchronous. Although breeding output is low, success rates are high due to co-operative feeding and defence against nest predators (Dow, 1978; Arnold, 2000). The "helpers" are male offspring of the breeding pair or siblings of the male of the

pair, and some helpers will attend multiple nests. Up to twenty males have been observed attending a single nest (Põldmaa and Holder, 1997).

Noisy miners are not alone among native species in their impacts on other species. The 2000 Action Plan for Australian Birds considers competition from 19 native birds to be a threatening process for already threatened Australian birds. Only 16 introduced species have been given this status in Australia (Garnett and Crowley, 2000). In spite of being a native species, the impacts of the noisy miner are now considered to be worse than those of the introduced common myna (*Acridotheres tristis*) (with which the noisy miner is often confused). The common myna has been found to threaten native species, particularly in the urban environment, largely due to competition for scarce breeding hollows (Pell and Tidemann, 1997; Grarock *et al.*, 2012). Their impacts, however, are not ubiquitous. A study in Sydney found that common mynas are no more aggressive than a number of native birds and appear to have little ecological impact other than being "passengers" of human-mediated habitat loss and degradation (Lowe *et al.*, 2011).

1.1.5 Managing noisy miner abundance and conserving small woodland birds

Managing noisy miners is about managing declining populations of small woodland birds. The conservation status of some small woodland birds in south-east Australia is critical (Paton and O'Connor, 2009; Ford, 2011a). Improving their status requires drastic action with

cessation of incremental clearing, lessening of grazing pressure and restoration of woodlands priorities for action. This includes the return of structural and spatial diversity: trees, shrubs, litter, ground cover and other elements in a patchy mosaic (Olsen et al., 2005, p2).

Reinstating economically productive landscapes to support functional ecosystems which approximate their pre-colonial condition is politically and practically difficult (Margules and Pressey, 2000). Restoration is particularly difficult when productivist and agrarianist narratives dominate public discourse (Botterill, 2006; Centre for Policy Development, 2015). Environmental management at a landscape scale is necessary if we are to move beyond the limitations of the Comprehensive-Adequate-Representative (CAR) reserve approach (Margules and Pressey, 2000; Lachapelle *et al.*, 2003). Recognising that many taxa are confronted by multiple threats can help environmental managers adopt systematic and prioritised conservation planning approaches which aim to apply a suite of measures to optimise biodiversity outcomes (Margules and Pressey, 2000; Auerbach *et al.*, 2015; Tulloch *et al.*, 2016b).

Aiding recovery of declining small woodland birds can be done in a number of ways. The federal listing of aggressive exclusion of small birds by noisy miners as a Key Threatening Process means that governments have a legal obligation to abate the threat. Abatements recommended in the listing include direct control of noisy miner abundance and revegetation (Department of the Environment, 2014).

The New South Wales Government Scientific Committee's listing of aggressive exclusion of small woodland birds by noisy miners as a Key Threatening Process acknowledges the synergistic role of three other Key Threatening Processes: clearing of native woodland, high-frequency fire, and invasion of native plant communities by exotic perennial grasses (NSW Scientific Committee, 2014). This listing considers revegetation to be the key solution in the long term. The committee opens the way for localised culling but recommends no co-ordinated state-wide control strategy because of local variation in the problem.

Doubts remain about the effectiveness and longevity of effect of culling noisy miners in the absence of habitat enhancement through revegetation. Recolonisation by noisy miners is likely to occur eventually, the rate depending on local connectivity to other source populations. Revegetation may be the single most effective action to increase colonisation by small woodland birds, but its impact may be enhanced when combined with control of noisy miners (Tulloch *et al.*, 2016b).

Multiple options are available to environmental managers seeking to abate the threat posed by noisy miners. The combination of options chosen in a particular locality will depend on local conditions, including available conservation resources, landscape configuration, extent of colonisation by miners, and extent of threat to small woodland birds. In the case of revegetation, a further consideration will be the balance between opportunity costs of foregone agricultural production and the value of increased economic and social benefits due to the revegetation (Ansell *et al.*, 2016).

1.1.5.1 Appropriate revegetation: political challenges, ecological traps and phase shifts

The Threat Abatement Plan proposed in the federal Key Threatening Process listing recommends

..... habitat alteration to increase the size and structural complexity of habitat patches to make them less accessible to noisy miners while providing appropriate habitat for other native bird species. Such measures include revegetation, to increase the size and/or connectedness of patches or to increase density of the shrub layer within patches, removal of

grazing or reducing fire frequency (Department of the Environment, 2014, p5).

Modelling of prioritisation of responses to the declines in small woodland birds in Australia's box gum grassy woodlands suggests that increasing tree cover is the most effective approach to increasing colonisation by small birds. It could create an average increase in colonisation by all species of 5% and by declining species of 11% (Tulloch *et al.*, 2016b). However, abating the threat posed by noisy miners through a revegetation campaign at a spatial, and particularly temporal, scale necessary to prevent further extinctions presents considerable political and logistical problems. The federal Biodiversity Conservation Strategy 2010-2030 called for 100 000ha of restoration in fragmented landscapes (Australian Government Department of the Environment, 2016). Nationally, however,

> Australia is still undergoing annual net losses of habitat, despite efforts to restore and revegetate. While this continues, we cannot meet our international obligations to protect our biodiversity (Paton and O'Connor, 2009, p2).

Following a change in vegetation clearing regulations, Queensland alone lost almost 280 000ha of native vegetation in 2013-14, most of the cleared land being used for agriculture (Sturmer, 2015).

Tepper (1896) considered that, in the interests of sustainable productivity, half of the agricultural landscape should remain under native vegetation. Lamenting broadscale clearing, he recognised the value of ecosystem services almost a century before the term was coined:

> Thus we have ruined our country by denuding hills and plains of all trees and shrubs under the idea of improving pastures and fields, and have destroyed their fertility by overlooking the fact that trees and shrubs are not only in the world for firewood and timber, for shade or ornament, at our convenience, but to create and maintain conditions permitting man to exist (Tepper, 1896, p6).

A more recent assessment suggests that in the interests of both productivity and conservation, 30% of the land surface of farms in grassy woodland regions of subtropical Queensland should be wooded (McIntyre *et al.*, 2004)

Successful revegetation must be carefully controlled and appropriate to conservation goals:

Degradation is so severe in many cases that it will not be overcome without active and ecologically appropriate intervention including mitigation of these causal problems and

reinstatement of indigenous biodiversity (McDonald et al., 2016, p1).

Additionally, due consideration must be given to spatial attributes of vegetation, the need for heterogeneity in age and type, and the interaction between replantings and remnants (Cunningham *et al.*, 2008; Cunningham *et al.*, 2014a; Lindenmayer *et al.*, 2016). *Ad hoc* planting risks creating ecological traps. An ecological trap is habitat preferentially occupied by organisms where they are unable to breed due to the adverse effects of ecological processes such as predation and competition. Ultimately, they may become extinct in the habitat. Ecological traps are particularly prevalent in modified landscapes (Battin, 2004; Belder *et al.*, 2018). The potential role of the noisy miner in creating ecological traps remains to be elucidated.

When ecosystems are stressed beyond their inherent resilience, they may move into new equilibria which require further input of energy to return them to their original state (Holling, 1973). Ecosystems displaying strong interspecific interactions are especially susceptible to threshold dynamics (Suding and Hobbs, 2009). The interaction of anthropogenic habitat modification and noisy miner colonisation is an example of a "critical transition" (Scheffer, 2009). The response of ecosystems has been non-linear, with small changes at patch or landscape scale precipitating big effects on avian assemblages. These alternative stable states may persist after the disturbance is removed (Scheffer and Carpenter, 2003; Mac Nally, 2008; Maron *et al.*, 2013). Such phase shifts are a particular problem in the highly modified agricultural landscapes of eastern Australia where small fragments and limited connectivity make sites inherently unstable and susceptible to threatening processes. As Dow (1977) indicates, presaging the concept of novel ecosystems,

> because so many of the reported cases of interspecific territoriality are of species living in habitats obviously disturbed or even created by man, these are probably not stable adaptations but rather dynamic social interactions between species that have perhaps only recently occupied such habitat (Dow, 1977, p119).

Hence, whilst long term, appropriate revegetation is a suitable, no-regrets measure for enhancing biodiversity in modified environments impacted by noisy miners, there may be situations where hysteretic effects mean that the chronic decline in native woodland and its associated avian assemblages cannot simply be reversed (Maron *et al.*, 2011). In some circumstances physical removal of noisy miners may be a necessary part of the process of biodiversity recovery.

1.1.5.2 Environmental management within a socialecological system

Conservation biologists work within tractable, bound systems to manage species and ecosystems for particular outcomes. At the same time, conservation biologists recognise that many of the threats to ecosystems and biodiversity lie in the wider social ecological system (Hobbs *et al.*, 2011; Lindenmayer, 2017). The ecological problem of noisy miners evolved over two centuries of habitat change within a wider social-ecological system in Australia.

As indicated in the previous section, one element of both conservation of small woodland birds and management of the negative effects of noisy miners is habitat restoration at a scale appropriate to the scale of the problem. A systems approach to conserving woodland biodiversity might also consider a more integrated interpretation of scale, to include other categories such as the social-ecological (Hobbs et al., 2011) (Figure 1). For example, agriculture is the single biggest historical source of loss and degradation of native habitat in Australia, occupying 58% of the nation's land surface (Australian Collaborative Land Use and Management Program, 2011). Clearing for agriculture is also the principal cause of current losses of biodiversity (WWF, 2015; Evans, 2016; Reside et al., 2019). The agricultural industry fulfils multiple social, economic and environmental roles in society. Current discourse about agriculture, however, is dominated by the productivist role of a deregulated industry within globalised, deregulated commodity markets (Tonts and Jones, 1997; Dibden et al., 2009; Muir, 2014; Centre for Policy Development, 2015; O'Keeffe, 2017). Notwithstanding growing interest in newer, ecologically holistic approaches to production such as regenerative agriculture (ABC TV, 2018; Massy, 2018), the current discourse is bolstered by narratives founded in agrarianism and a "feed the world" mythology (Botterill, 2009; Muir, 2010; Berry et al., 2016). Transforming the discourse to incorporate other values of land, such as conservation, is a difficult task (Hobbs et al., 2011). Since the influence of conservation biologists on the wider social-ecological system is limited, they mostly operate at the smaller spatial and social scale represented by finite units of habitat such as patches, reserves, exclosures, ecosystems, and landscapes.

The role of the wider social-ecological system is crucial to the noisy miner story. Where continuing clearing of native woodland and forest in eastern Australia creates fragmented woodland and new forest edges, it is potentially increasing the area of habitat suitable for noisy miner colonisation. Appropriate revegetation can deter noisy miner colonisation and support small woodland birds. However, revegetation is a longer-term strategy and engaging with land use policy at state or federal level to slow loss and increase restoration is difficult politically. Removing noisy miners is a potentially quicker method of supporting small woodland birds so there is currently a great deal of interest in this method.

The decline of small woodland birds, as with most ecological problems, is the result of multiple threatening processes whose genesis has as much to do with political and economic influences as ecological. In this study, I consider the effects of only one threatening process over which it was possible to exert some level of control at the scale of the study: abundance of noisy miners.

1.1.5.3 Theoretical bounds of the study: the distinction between science and values

Within the modern canon of ecological thought, intervention in ecosystems altered by human activities to achieve conservation goals is the dominant management approach. The grounds for intervention have shifted over time from a belief in the need to maintain some wild areas to protect threatened species, to a recognition of human dependence on ecosystem services within a broader definition of the environment as a social-ecological system (Millennium Assessment Board, 2005; Mace, 2014; Díaz *et al.*, 2018).

One form of intervention widely practised is the lethal control of populations of species deemed undesirable due to their impacts on other species (Parkes and Murphy, 2003; Gregory *et al.*, 2014). Undesirable species are commonly divided into two groups according to their provenance (Low, 2007; Davis *et al.*, 2011; Schlaepfer, 2018; Gbedomon *et al.*, 2020). Undesirable exotic species are described as "invasive", connoting increases in both population and range (Kearney *et al.*, 2018). Foreign provenance alone, in the absence of proven ecological impacts, is often sufficient to deem an exotic species undesirable (Lowe *et al.*, 2011). Exotic species with major ecological impacts but "desirable" economic benefits are tolerated or supported (Hunt *et al.*, 2007). In Australia, commercial grazing of native vegetation by exotic herbivores covers 45% of the continent's land surface and has resulted in major ecological changes (Alex and John, 2007).

Native species deemed undesirable by virtue of their abundance are described as "overabundant" (Garrott *et al.*, 1993; Nugent *et al.*, 2011). Undesirability based on overabundance may be due to economic impacts, such as competition between wild and domestic herbivores (Fennessy, 1966; Dawson and Munn, 2007), or to impacts on biodiversity (Lunney *et al.*, 2007; Livezey, 2010).

How we define and manage undesirable species is contested (Ramp and Bekoff, 2015; Driscoll and Watson, 2019; Hampton *et al.*, 2019; Rohwer and Marris, 2019). Indeed, the fundamental belief that the principal goal of conservation biology should be to conserve indigenous biodiversity and eliminate foreign species is an expression

of a values system that is contested. It is contested both within conservation biology (Low, 2002; Davis *et al.*, 2011; Bowman, 2012; Flannery, 2019) and by other sectors of society with different priorities (Baynham-Herd *et al.*, 2018). Values systems based on human exceptionalism or the need for continued economic growth, for example, generally do not see value in other species or the natural environment other than as instruments of human development. The contrast between a belief in nature's instrumental value and a belief in inherent value is a further source of contestation (Nelson and Vucetich, 2012).

I recognise the breadth and value of these different ethical approaches to conservation, and their relevance to the contestable ethical principles upon which the culling of noisy miners is founded. The scientific method is the best source of evidence for the consequences of a particular action, or of failing to execute a particular action. However, the decision as to whether an action should or should not be carried out is dependent on much more than scientific knowledge. Such decisions are made within a "decision context" - the institutional, political and social context within which values, rules and knowledge interact to create or influence conservation policy, research and praxis (Gorddard et al., 2016; Wyborn et al., 2016). The established decision context may be determined by a narrow range of views from academics, conservation organisations and government departments, supported by a dominant discourse that largely excludes other views, and reinforced by funding allocations that perpetuate a particular approach to conservation research (Dryzek, 2013; Dryzek and Pickering, 2018). The established decision context is not the only one: other sectors of society may have different sets of values, rules and knowledge. Co-production of conservation policy - broadening the established decision context by incorporating other values, rules and knowledge - is one method of managing conflict and, ultimately, ensuring more successful conservation outcomes in a changing world (Colloff et al., 2017; Wyborn et al., 2019). Such exploration is beyond the simple dichotomies presented by scientific appraisal of action or inaction. Hence, whilst the role of science is indispensable in contributing to the knowledge of any given decision context, science alone is insufficient in deciding what should be done.

A full treatment of these topics is beyond the scope of this thesis, however. I therefore begin from the generally accepted belief in conservation biology today that maintaining biodiversity is a "good" thing and that more native biodiversity is "better" than less (Soulé, 1985). The purpose of my study was to provide information about the effectiveness of culling noisy miners such that decisions based on evidence rather than belief might then be made by society.

1.1.5.4 Culling: intuitively attractive, not necessarily effective

Intervention to reduce abundance of overabundant or invasive species directly through translocation or culling is a common, and intuitively attractive, response (Clarke and Schedvin, 1997; Livezey, 2010; Kierepka *et al.*, 2017; O'Loughlin *et al.*, 2017). However, the costs and outcomes of such interventions are often ineffectively monitored (Rothstein and Peer, 2005; Treves and Naughton-Treves, 2005; Livezey, 2010; Nugent *et al.*, 2011) and compensatory mechanisms are common (Dexter *et al.*, 2013; Lazenby *et al.*, 2015; Kierepka *et al.*, 2017). Such mechanisms can lead to unexpected or perverse outcomes and result in wasteful application of scarce conservation resources (Kosciuch and Sandercock, 2008; Bergstrom *et al.*, 2009; Bodey *et al.*, 2011; Marlow *et al.*, 2015; Doherty and Ritchie, 2017). Before culling is applied at a broader scale, managers need to have as much information as possible about likely outcomes, costs and responses of both the species to be culled and target species (Figure 1).

Numerous attempts to control noisy miners through culling or translocation have been made in fragmented agricultural landscapes of eastern Australia in the last two decades. The results of four studies have been published (Grey et al., 1997; Grey et al., 1998; Debus, 2008; Davitt et al., 2018). The published studies report varying levels of recolonisation by noisy miners but also report some increases in detection rates of small woodland birds after removal of noisy miners. These studies had a number of limitations, however. The first two, carried out in the 1990s, used only three and four replicates respectively and measured detections rates of all woodland birds, including some that are able to coexist with noisy miners (Grey et al., 1997; Grey et al., 1998). An unofficial cull begun in the same decade was on only one site, had no control, culling was ongoing, costs were covered by the landowners, and results were confounded by simultaneous revegetation (Debus, 2008). Such conditions are unlikely to hold in any large-scale application of culling as a management response. The most recent experimental cull, completed at the same time as that reported in this study, was conducted at a larger scale and recorded rapid recolonisation of sites by noisy miners (Davitt et al., 2018). All published studies used the same metric of success, detection rates of woodland birds. Detection rates are an incomplete measure of ecosystem function as they do not distinguish between presence of a species in a site and use of that site by the species. Finally, prior knowledge of likely costs is essential to assess cost-effectiveness before applying management techniques more broadly. Only one of the previous studies reported costs (Clarke and Grey, 2010).



Figure 1. Ecological and practical knowledge required before embarking on large scale culling programs of overabundant and invasive species (concept: C. Foster)

A fifth study controlled noisy miners to reduce aggression against and nest disruption of the critically endangered Regent honeyeater (Crates *et al.*, 2018). Unlike studies in fragmented agricultural landscapes, recolonisation by noisy miners post cull did not occur, most likely due to a lack of connectivity to cull sites. Hence, limited inference can be made from the experience in that landscape to the fragmented agricultural landscape where noisy miners exert their biggest effect spatially on avian biodiversity.

Many of the unpublished cull attempts were small scale, unreplicated interventions on private land and had differing levels of success. A metastudy is now under way to consider the results of all cull attempts, published and unpublished, with the aim of indicating conditions under which culls are most likely to be successful (C. Melton, personal communication, 2018).

In summary, small woodland birds suffer the impacts of multiple threatening processes. Empirical evidence that managing just one of these threats, noisy miner aggression, will have beneficial ecological outcomes for small woodland birds is limited. Bird populations are a function of the balance between rates of immigration, emigration, survival and reproduction. Doubts remain as to the mechanisms by which interspecific competition interacts with each of these factors. Whilst it appears that the aggressive behaviour of noisy miners limits the access of small woodland birds to fragments of native woodland, it is not clear whether small birds will use those fragments post-cull. The possibility exists that vegetation configuration at patch or landscape scale remains a hidden constraint to foraging or nesting by smaller birds. In addition, uncertainties remain regarding the rate of recolonization by noisy miners post-cull and whether other large, aggressive bird species will become dominant following culling, with consequent negative impacts on smaller birds. Finally, little is known about the relative costs and benefits of culling compared to other possible management options such as revegetation. The aim of this study was to fill these many knowledge gaps.

1.1.6 Study aims

The study consisted of two broad components (Figure 2). The first was an empirical study designed to test the effects of an experimental cull of noisy miners on ecosystem function (Chapters II - IV). The second was a historical review of cultural references to the noisy miner since the European invasion of the continent to see how changing cultural attitudes reflect the changing ecological role of the species (Chapter V).

Field experiments: Chapters II - IV		
Outputs: effect of the cull on noisy miners	Outcomes: effect of the cull on target species	
	Chapter III : An empirical test of the mechanistic underpinnings of interference competition	
Chapter II : Patch-scale culls of an overabundant bird defeated by immediate recolonisation	Key question : Can culling noisy miners improve foraging opportunities and reduce harassment for small woodland birds?	
Key question : is culling a cost-effective method of reducing abundance of noisy miners?	Chapter IV : An experimental test of a compensatory nest predation model following lethal control of an overabundant native	
	Key question : Can culling noisy miners improve breeding success of small woodland birds through reducing nest predation?	
Cultural history: Chapter V		
Native to nemesis: a cultural history of the noisy miner		
Key Question : have cultural attitudes to the species changed in line with the change in the species ecological role?		

Figure 2. Structure of thesis and key research questions

1.1.6.1 The empirical study

I completed a controlled experimental cull of noisy miners in eight small patches of woodland in a highly modified agricultural landscape of south eastern Australia. Such a landscape is typical of the sub-continental region over which noisy miners now predominate. My purpose was threefold. First, I wished to assess the effectiveness and feasibility of patch-scale culling as a practical management intervention that could be applied at a broad scale to lower noisy miner abundance (Chapter II). Second, I wished to see if reducing noisy miner abundance improved ecosystem function and, in particular, whether such a reduction benefitted small woodland birds (Chapters III and IV). Third, I sought to elucidate some of the ecological mechanisms by which noisy miners exert their impact (Chapters III and IV).

My BACI (before-after-control-impact) design aimed to assess the effect of the cull on ecological function of sites rather than solely on detection rates of other woodland birds. Here I distinguished outputs from outcomes: as well as monitoring noisy miner abundance, I devised additional metrics for outcomes which indicated use of sites post-cull by small woodland birds. Monitoring was conducted from nine months before the cull to twelve months after.

The resource availability theory of competition posits that interference competition limits access of less competitive species to resources and forces them to waste energy evading aggression from more competitive species. I monitored foraging rates of small woodland birds to see if removing noisy miners improved access to foraging resources (Chapter III). Noisy miner abundance is correlated with an avian assemblage that includes many large, aggressive generalist species (Thomson *et al.*, 2015). I therefore also monitored harassment rates of small woodland birds. The purpose here was threefold: to assess the amount of harassment carried out by noisy miners; to see if small woodland birds suffered less overall harassment after the cull; and, given the important role of noisy miners in structuring avian assemblages, to indicate if there was any compensatory aggression by other species post-cull.

I also sought to assess any post-cull change in breeding potential of small woodland birds, since successful breeding is a population process essential for the recovery of declining species (Chalfoun *et al.*, 2002; Johnson, 2007) (Chapter IV). In this landscape, nest predation is the principal cause of breeding failure and birds are the principal nest predators (Zanette and Jenkins, 2000). However, measuring breeding of small woodland birds in sites colonized by noisy miners is problematic: few small woodland birds manage to breed due to nesting disruption by noisy miners (Low, 2014). I therefore conducted artificial nest predation experiments with camera monitoring before and after the cull. Whilst such experiments are imperfect analogues of real breeding (Major and Kendal, 1996; Zanette, 2002; Thompson and Burhans, 2004), they are the only way of empirically indicating any change in nest predation following the cull. The study landscape supports many nest predatory bird species so this part of the study aimed to show the proportion of nest predatory responses by other species.

1.1.6.2 The historical dimension

Managing the trajectory of ecosystems toward desired outcomes requires an understanding of the means by which they developed (Lindenmayer et al., 2008, p 129). The ecological problem represented by noisy miners developed over two centuries of landscape change. The historical record of the noisy miner in newspaper articles from the 1830s to the present shows a marked change in cultural attitude to the species. In less than two centuries, the species has shifted from a "gallant little bird" (Anon, 1878) and frequent subject of popular poetry to "the mafia of the bird world", a "bully" and a "despot" (Clarke, 2004; Birds in Backyards, 2011; Maron *et al.*, 2013; Loyn *et al.*, 2016). I posit that the change in cultural attitudes reflects the change in the species ecological role. Whilst early records note the aggressive tendencies of noisy miners, the first reports of the ecological impacts of the species only appear in the post-war period of rapid economic and agricultural development. This suggests that during the post-war phase of extreme levels of clearance of native vegetation in eastern Australia, landscape transformation reached critical levels where noisy miners began to have an impact on small woodland birds. This topic is considered further in Chapter V.

1.1.7 Study region

The field experiments reported in Chapters II, III and IV were conducted between 2015 and 2017 on small (average 13ha) fragments of eucalypt woodland on private farmland in the highly modified agricultural landscape of the South West Slopes Bioregion of New South Wales (Figure 1 Chapter 2). The study region has a continental temperate climate with hot summers and cold winters. Average annual rainfall is 624 mm (Gundagai) and 526 mm (Junee) (Bureau of Meteorology, 2017). The region is typical of the kind of landscape heavily colonized by noisy miners in the sheep-wheat belt of eastern Australia from South Australia to southern Queensland. The sheep-wheat belt lies inland of Australia's Great Dividing Range, conforming roughly with the original range of temperate woodland (Yates and Hobbs, 2000).

Eighty per cent of the original extent of native vegetation in the South West Slopes Bioregion has been cleared, primarily for agriculture (Benson, 2008). The majority of remnant woodland is on private land with conservation tenures occupying 2.28% of the total land area (Office of Environment and Heritage 2015). White Box-Yellow Box-Blakely's Red Gum Grassy Woodland, the dominant remnant vegetation type in the study region, originally covered several million hectares. Remaining fragments cover 405 000ha and the vegetation type is now listed as a critically endangered ecological community (Department of Environment, Climate Change and Water, 2010).

The region has been the subject of a long-term ecological monitoring program by the Australian National University since 2000 (Cunningham *et al.*, 2008). Diversity and abundance of birds in the region is correlated with native vegetation cover (Cunningham *et al.*, 2014b) with noisy miners favouring areas of lower cover. Whilst the region is dominated by noisy miners and other larger species associated with noisy miner colonization, some ecological restoration has occurred over the period of the monitoring program with consequent improvements in detection rates of a number of small woodland birds (Cunningham *et al.*, 2014a; Lindenmayer *et al.*, 2016).

1.1.8 Summary of outcomes

Chapter II: Patch-scale culls of an overabundant bird defeated by immediate recolonisation.

In this chapter I consider the effect of the cull on noisy miner abundance. The principal finding of the experiment was the unexpected, immediate compensatory immigration by noisy miners into treatment sites after each of two culls performed within four weeks of each other. Over the full period of the study, modelled mean abundance of noisy miners was 25% lower in treatment sites than in control sites post-cull. Noisy miner abundance in all sites remained three to five times higher than the ecological impact threshold of 0.6 individuals/ha, however. The cull cost AU\$24 per bird and AU\$136 per hectare of woodland cleared of noisy miners. This is 18 times lower than the cost of revegetation, but the cull was largely ineffective. The outcome provides empirical evidence that in this highly fragmented agricultural landscape with high densities of noisy miners, patch-scale culling is not a cost-effective solution. One can infer from this study that patch-scale culling is likely to be ineffective over most of the agricultural region of eastern Australia where the impacts of noisy miners are greatest.

Chapter III: An empirical test of the mechanistic underpinnings of interference competition

This part of the study was designed to indicate if small woodland birds were able to make better use of treatment sites for foraging after the cull. I measured foraging and harassment rates in the breeding seasons before and after the cull. Aggressive interspecific interactions were common. I recorded 253 harassment events by a total of 24 bird species. Forty-one bird species were victims of harassment. Noisy miners were responsible for 66% of recorded harassment events. I observed foraging by 17 species of small woodland bird at an average rate of 4.5 foraging events per hour per 2ha site but, foraging detection rates were below 13%
for all species in the pre-cull phase. Over the period of the study, noisy abundance in treatment sites declined by 34% relative to control sites as a result of the cull. Noisy miner abundance remained above ecological impact thresholds in all sites throughout this period. Nonetheless, the cull disrupted intraspecific relations of this socially complex species, so I expected some effect on the responses of small woodland birds. Foraging rates of small woodland birds doubled in treatment compared to control sites post-cull. This increase was largely due to the four most commonly seen species, which seemed able to co-exist with noisy miners. Paradoxically, I recorded no change in harassment rates in spite of the increase in foraging rates. The chapter indicates that culling noisy miners may improve access to foraging resources for some species of small woodland birds up to 251 days post cull. Most species of small woodland birds recorded saw no benefit, however.

Chapter IV: An experimental test of a compensatory nest predation model following lethal control of an overabundant native

This part of the study aimed to show whether removing noisy miners has the potential to improve breeding outcomes for small woodland birds. Nest predation is the principal cause of nest failure in this landscape and birds are the main nest predators. Noisy miners are only one among many nest predators, however. I measured artificial nest predation rates in the breeding seasons before and after the cull. Over this period, noisy miner abundance declined by 34% in treatment compared to control sites due to the cull. Noisy miners were responsible for 18% of nest predator where the predator was identified but I identified five other nest predatory bird species. I detected no significant change in artificial nest predation rates post cull which suggests compensatory nest predation by other species. There was no significant change in identity of nest predators. This outcome suggests that culling noisy miners is unlikely to reduce nest predation rates for small woodland birds.

Chapter V: Native to nemesis: a cultural history of the noisy miner

The noisy miner was known and named by many indigenous groups. The species subsequently became a common subject of popular culture during the colonial period. Using the National Library of Australia's online data archive "Trove", I discovered almost 3000 historical references to the species. These

references included paintings of the species completed within four years of the arrival of the Frist Fleet in 1788. Local and national newspapers published stories, poems and letters about the species. The popular "nature notes" format included many observations of noisy miners' foraging and breeding behaviour as well as interactions with people. A striking finding was the contrast between the frequently positive sentiments for the species right up until the post-war period and more recent references to the species as a "despot", "bully" and "mafia of the bird world" (Clarke, 2004; Birds in Backyards, 2011; Maron *et al.*, 2013; Loyn *et al.*, 2016). Through exploration of historical references to the species over the colonial and modern period, I show that there has been a marked shift in cultural attitude to the species in parallel with its changed ecological role.

This chapter improves our understanding of the historical social-ecological changes that have fostered the transformation of a natural ecosystem process, interspecific competition, into a Key Threatening Process. As such I offer the chapter as an antidote to environmental amnesia.

1.2 Synthesis

1.2.1 Summary of research results

I conducted an experimental cull of the overabundant native honeyeater, the noisy miner, in patches of remnant woodland with the aim of discovering if this management intervention can improve ecosystem function for declining small woodland birds. Immediate recolonisation by noisy miners from surrounding habitat meant that I was unable to reduce their population below ecological impact thresholds. There was a small but statistically significant reduction in noisy miner abundance in treatment sites compared to control sites. Some species of small woodland bird foraged more in treatment compared to control sites post cull, but I detected no change in the amount of harassment they experienced. Artificial nest predation rates did not change after the cull.

1.2.2 Significance of findings

Much of our knowledge about the ecology and impacts of noisy miners is based on modelling of large datasets of bird detection (Mac Nally *et al.*, 2012; Thomson *et al.*, 2015). In contrast, this study provides empirical evidence of what happens when noisy miners are removed from individual woodland patches. Such evidence is vital for the efficient deployment of limited conservation resources. By monitoring metrics beyond simple detection, I showed both the potential benefit to small woodland birds of culling noisy miners and derived an indication of the mechanism by which noisy miners impact small woodland birds.

I showed that culling noisy miners in the study landscape is not a cost-effective management intervention for reducing their abundance, nor does culling offer great benefits for declining small woodland birds. The level of fragmentation and degradation of native woodland in the study area is representative of a large area of eastern Australia's sheep-wheat belt. We may infer that similar outcomes would occur in other parts of the region. Indeed, a recent culling experiment in northern New South Wales experienced similar rapid recolonisation (Davitt et al., 2018). Noisy miners are an ecological problem across their range of 1.3 million km² (Higgins et al., 2001). This range includes non-agricultural areas such as urban and suburban zones, forest edges and planted wildlife corridors (Catterall et al., 1991; Hastings and Beattie, 2006; Parsons et al., 2006; Maron et al., 2013). The sheep wheat belt, however, covers over one million km² and is the largest single landscape type over which noisy miners exert ecological impacts. In such landscapes, alternative methods of managing noisy miners and supporting small woodland birds must now be sought. The most promising of these methods is ecological restoration, with attention to re-creating the structural complexity of intact woodland, in particular a shrub layer (Hastings and Beattie, 2006; Lindenmayer et al., 2010b; Lindenmayer et al., 2012; Ikin et al., 2018; Lindenmayer et al., 2018)

1.2.3 Limitations of the study

The principal limitation to successful assessment of post-cull changes in ecosystem function was the inability to reduce noisy miner abundance sufficiently. The small reduction in noisy miner abundance achieved in treatment relative to control sites (28% from the pre-cull to post-cull breeding season; 25% over the full duration of the study) may have been too small to detect any compensatory harassment or nest predation effect. Noisy miner densities in all sites remained above the published ecological impact thresholds of 0.6 - 0.8 birds/ha (Mac Nally *et al.*, 2012; Thomson *et al.*, 2015).

A possible criticism of the study is the failure to continue culling until recolonisation slowed. No doubt recolonisation would eventually have completely stopped when all birds within their maximum relocation distance had been removed. There are, however, ethical questions and possible ecological risks associated with eradicating a strongly interacting native species from a locality. The decision not to continue culling after two attempts was made primarily because the experiment had a very practical purpose. It was designed to test the feasibility of culling noisy miners as a management intervention that could be applied in the real world. In the case of noisy miners, this means culling at a large scale. I considered that prohibitive costs would mean that culling could not be applied at a large scale if it had to be repeated numerous times.

The decision to cull at patch scale also reflected this practical purpose of the study. Patches were chosen as tractable units of habitat within functioning farms that could feasibly be cleared of noisy miners. I assumed that a colony was confined to a patch of woodland as it was difficult to imagine birds maintaining coherent social relations across hundreds or thousands of metres of open agricultural land between patches. Previous estimates put noisy miner home range at about 200m (Dow, 1979). Given the amount of post-cull recolonisation into patches separated from neighbouring patches by much more than 200m, I considered that recolonising individuals most likely came from other colonies in patches outside the culled patch. It may be, however, that home range in this landscape is greater than that reported in Dow's studies in the northern part of the species' range. It may also be that colonies extend across more than one patch. There is continuing lack of basic knowledge of noisy miner ecology, including home range, the conditions under which they choose to relocate when habitat becomes available following culling, and the scale at which birds are willing to relocate. These factors are significant for two reasons. The first is that the range at which noisy miners are willing to recolonise is a determinant of the scale of culling required to prevent recolonisation. The second is that post-cull interspecific behaviour of these socially complex birds may be influenced by whether recolonising individuals come from the same metapopulation or a different one. This study was not designed to track movements or origins of recolonising individuals. Genetic analyses of culled birds and banding of birds from coteries across the wider landscape could improve our knowledge of the origin of recolonising birds.

Other configurations of culling have been proposed by ecologists. In a "doughnut" approach, culling takes place at the core of a larger patch but spares coteries nearer the edge. It has been suggested that this method can create a noisy miner-free core whilst the individuals that remain near the edge deter recolonisation of the patch. However, such an approach requires patches large enough to distinguish a core from edges. In the landscape of this study, patches were too small (mean = 13ha), and coteries too mobile within patches, to distinguish edge birds from core birds. In a "mosaic" approach, culling is done in selected patches across a landscape to lower abundance at a local or district scale beyond the patch. How long such methods prevent recolonisation remains unknown but the complexity of exploring different culling configurations was beyond the scope of this study.

An option when we have uncertainty about the outcome of a management action is to conduct it within an adaptive management framework, iteratively updating the action as outcomes become apparent over time. Such an approach could be applied to noisy miner management but is less suited to the constrained timeline of a PhD.

The success of many field-scale ecological studies is limited by the inability to monitor a sufficiently large sample size to detect an effect (Steel *et al.*, 2013; Martínez–Abraín, 2014). Sample sizes are, in turn, constrained by availability of time and money. Stringent site requirements in this production landscape were the chief limitation to a bigger sample size in my study. I required landowners willing to host the study; availability of at least two woodland patches similar in vegetation characteristics on each farm to act as treatment and control; consistent detection of noisy miners; and farms sufficiently close together to allow all surveys to be completed within a few days of each other. Fulfilling all these requirements meant that the study was finally conducted on eight treatment/control replicates spread across seven farms.

The small sample size was a particular problem when trying to detect possibly subtle effects of the small change in noisy miner abundance post-cull. For example, artificial nest predation rates declined in treatment compared to control sites post cull, but the change was not statistically significant (Figure 3, Chapter IV). With greater resources, the study could have been conducted on more farms over a larger area. It is possible that more treatment effects would then have been apparent.

This study was designed to examine the effect on small woodland birds of changing just one condition, noisy miner abundance. As a result, I required all sites to contain colonies of noisy miners. Because of noisy miner habitat preferences for fragmented, degraded landscapes, this requirement may have selected for sites less likely to support populations of small woodland birds. As a result, sample sizes of foraging and harassment of small woodland birds were small across sites and treatments. Out of a total of 253 harassment events, I recorded only 41 against small woodland birds and these events were distributed across the two phases and two treatments. With such a small sample, I was unable to detect a significant change in harassment rates of small woodland birds post-cull (although the direction of the change was positive; see Figure 3, Chapter III). A solution would have been to include some less degraded sites in the study to serve as baselines for presence of small woodland birds and then to conduct a more stratified analysis of responses. My study was nested within the large sample of sites that have been monitored since the early 2000s in the Australian National University's South West Slopes Restoration Study (Cunningham et al., 2014a). Some of those study sites have more intact vegetation structure, hence, fewer noisy miners and greater detection rates of small woodland birds so the possibility exists of repeating the experiment with a more stratified set of sites (Belder *et al.*, 2018).

Technological advances such as infra-red activated cameras permit efficient collection of large amounts of data but can present their own challenges (Cox et al., 2012). My attempt to apportion artificial nest predation between the different species of nest predators, and then assess any post-cull change in proportion of nest predation conducted by each predator, depended on successful camera capture of nest predators. Artificial nests were often among highly mobile foliage in an extremely hot environment (temperatures in study sites at times exceeded 40 Celsius). Consequently, hundreds of thousands of photos of moving leaves were taken whilst at times the cameras were unable to distinguish the temperature difference between nest predators and background so failed to capture a predator. I deployed 576 artificial nests and monitored 268 with cameras. 132 of the monitored nests were predated but I was able to identify a nest predator in only 60 cases. At 45%, my camera capture success rate (number of predated nests where the predator was identified/total number of predated nests monitored by camera) was better than other studies in the region (Robertson et al., 2014; Okada et al., 2017). Nonetheless, with only 60 identified nest predations split between two phases and two treatments, useful analysis of trends was limited.

Part of the problem here was the need to procure cameras from wherever possible, meaning that over the course of the study I used a total of eight different models. Sticking to one model and getting to know its characteristics better would likely improve capture rates.

1.2.4 Conclusion

This research project has shown the limitations of focussing solely on reducing the abundance of an overabundant species to manage its ecological impacts. Most ecological problems arise from a combination of threatening processes and addressing only one is rarely the best approach to management. Small woodland birds are subject to a range of threats that have led to their decline. I have shown that, due to immediate recolonisation, removing noisy miners is unlikely to be of great benefit.to small woodland birds in areas with similar characteristics to the highly fragmented agricultural landscape of this study. Whilst there is some potential increase in foraging opportunities for small woodland birds, I found that the benefit was species-dependent, and I cannot be sure that the positive effect will be long term. This increase in foraging opportunities was not accompanied by a reduction in harassment rates. Successful breeding is essential for recovery of declining small woodland birds, but my study shows nest predation rates are likely to remain high even after controlling noisy miners.

Overabundant and invasive species are among the greatest threats to biodiversity globally, particularly when their impacts interact with habitat modification (Nugent et al., 2011; Mac Nally et al., 2014; Kearney et al., 2018). Culling is a common management response but it is not always successful and many culls are conducted without clear formulation of outputs and outcomes, monitoring may be poor or absent and costing is often overlooked (Rothstein and Peer, 2005; Treves and Naughton-Treves, 2005; Livezey, 2010; Nugent et al., 2011). Compensatory ecological processes are common and unexpected or perverse outcomes are possible (Dexter et al., 2013; Lazenby et al., 2015; O'Loughlin et al., 2017). My study showed the importance of having clear empirical evidence of the likely outcomes of culling before expensive management interventions are applied at a wider scale (Figure 1). The unexpected outcome of immediate recolonisation in this study highlights the importance of a prior understanding of a species' basic ecology, including home range. In the case of colonial species such as the noisy miner, knowledge of the spatial extent of colonies in relation to vegetation configuration is essential. Where recolonisation from surrounding areas is a risk, we need to know the conditions under which individuals or colonies are likely to recolonise and how vegetation configuration at patch and landscape scale influence this (Figure 1).

Continued clearing of native vegetation and the production of forest edges is a global problem for vertebrates (Pfeifer *et al.*, 2017). As clearing continues in Australia, it is likely to create further opportunities for colonisation by noisy miners or other colonial *Manorina* species and a consequent niche reduction for small woodland birds (Mac Nally *et al.*, 2014). Interventions by conservation biologists beyond the biotic/abiotic level of ecosystems are necessary if these large-scale impacts on the natural environment are to be curbed in the future. This means engaging with the wider social-ecological system that permits continuing deforestation, and with social and policy settings (Hobbs *et al.*, 2011; Lindenmayer, 2017; Woinarski *et al.*, 2017).

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Chapter 2: Patch-scale culls of an overabundant bird defeated by immediate recolonization

Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with https://policies.anu.edu.au/ppl/document/ANUP_003405

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multiauthor papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

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Foreword

This chapter considers the effect of the experimental cull of noisy miners on the direct output of the study, noisy miner abundance, and considers the costs of achieving a given level of population reduction. Noisy miners structure avian assemblages at noisy miner densities above 0.6 - 0.8 individuals/ha so it is important to know if culling them is a cost-effective method of reducing noisy miner density below such thresholds. Compensatory ecological processes such as immigration are common after culling so it is also important to know if such processes affect the success of population reduction through culling.

Abstract

Overabundant native animals cause a variety of human-wildlife conflicts which can require management to reduce their social, environmental or economic impacts. Culling is an intuitively attractive management response to overabundance but poor monitoring of results and costs means that evidence for successful outcomes is often lacking. Furthermore, many culls worldwide have been ineffective or counterproductive due to ecological release mechanisms or compensatory responses by the overabundant species. We completed a controlled, replicated, costed and rigorously monitored experimental cull of the endemic Australian honeyeater, the noisy miner (Manorina melanocephala). Aggressive exclusion of birds from remnant woodland patches by overabundant noisy miners is listed as a Key Threatening Process under Australian conservation legislation due to its impacts on threatened birds. The problem is particularly prevalent in the highly modified agricultural landscapes of eastern Australia. The species impacts avian assemblages at low densities (0.6 - 0.8 birds/ha) and at a sub-continental scale (>1 million km²). Some ecologists recommend culling as the only management response capable of timely reversal of declines of threatened small woodland birds. We monitored noisy miner abundance before and for twelve months after a culling program and found that immediate recolonisation from the surrounding landscape negated the impact of the cull. We hypothesise that this is due to a vacuum effect whereby birds resident in more marginal habitat around treatment patches move into the vacant territory post-cull. Modelled mean abundance of noisy miners declined by 22% in treatment sites compared to an increase of 4% in control sites in the post-cull period. Abundance in all sites, however, remained 3-5 times higher than published ecological impact thresholds. Return on investment analysis indicated no relationship between culling effort and reduction in noisy miner abundance. We conclude that culling at a patch scale is not an efficient method of reducing noisy miner abundance to levels unlikely to impact threatened woodland birds in the highly modified study landscape, despite estimated costs 18 times lower than another potential management response of revegetation. Our study highlights the importance of building empirical evidence before intuitively attractive but not necessarily ecologically effective management responses are applied more widely.

Keywords

Overabundant native species, *Manorina melanocephala*, evidence-based environmental management, cull, population control, threat management, ecosystem recovery, interspecific competition, ecological release, compensatory immigration

2.1 Introduction

Changes in distribution and abundance of native animals in response to anthropogenic habitat modification and other threatening processes are not uniform. Whilst many species are declining (Ceballos et al. 2017), some species have increased to the point of overabundance (Garrott et al. 1993, Foster et al. 2014, Mac Nally et al. 2014). Overabundance means that the animal's population is greater than the ecological (Caughley 1981) or cultural (Dubois et al. 2017) carrying capacity in a given environment. Ecological problems associated with overabundance of native species, such as impacts on co-existing species and the disturbance of ecological equilibria, have been reported in multiple geographic locations and across taxa (Garrott et al. 1993, Mendelssohn and Yom-Tov 1999, Nugent et al. 2011). Impacts on threatened species are likely to become worse as climate change interacts with habitat modification and interspecific competition (Bennett et al. 2015). To manage overabundant species efficiently for conservation outcomes, we need clear guidance about which actions are most likely to reduce their impacts (Tulloch et al. 2017), and how much effort is required to do so (Auerbach et al. 2014).

Management responses to overabundant native species have included diversionary feeding (Kubasiewicz et al. 2016), fertility control (Nugent et al. 2011), translocation (Clarke and Schedvin 1997) and lethal control (Newsome et al. 2017). Culling has been used to manage populations of overabundant native herbivores to protect habitat quality (Nugent et al. 2011); to reduce predation on bird species of conservation concern (Livezey 2010); to control brood parasitism of endangered songbirds (Rothstein and Peer 2005); to reduce declines in a threatened bird species through hybridisation (O'Loughlin et al. 2017); and to reduce competition from aggressive bird species (Clarke and Schedvin 1999, Debus 2008).

Since the impacts of many overabundant species are a function of population density (Carter et al. 2007, Foster et al. 2014), it is intuitively attractive to reduce or eliminate the population through lethal control. However, for a culling program to be effective and lasting, we need clear knowledge of the relationship between the density of the overabundant species and its ecological impacts, and knowledge of the temporal and spatial scale of control required (Lieury et al. 2015, Kierepka et al. 2017) so that we can formulate effective population reduction targets. We also need to know the costs of achieving such targets so that scarce conservation resources can be efficiently allocated. To ensure the effects of the cull are not nullified by compensatory processes such as immigration or reproduction, we also need a good understanding of the ecology of the overabundant species and its likely response to culling (Kierepka et al. 2017, Newsome et al. 2017). A species' population dynamics and behavioral ecology, for example, determine which life stage has the most

influence on population growth (Zipkin et al. 2009, Lieury et al. 2015) and whether culling acts as compensatory or additive mortality (Sandercock et al. 2011). Obtaining information is costly, so at times we are forced to make use of existing knowledge based on expert elicitation or models (Tulloch et al. 2016). However, intuition, expert elicitation, and modelling need to be tempered with empirical evidence of effectiveness and costs before conservation resources are committed to a broader management response (Treves and Naughton-Treves 2005, Zipkin et al. 2009).

Reporting on the effectiveness and costs of conservation management programs, including culls, and their comparison with alternative management strategies, is inconsistent (Rothstein and Peer 2005, Livezey 2010, Nugent et al. 2011). Limited information exists on a regional or global scale to inform managers whether culling is a cost-effective option for reducing overabundant native populations. Experimental studies or monitoring of management actions are the best source of such information but a lack of adequate monitoring to test the impacts of actions is a problem in many culling programs (Treves and Naughton-Treves 2005) and in conservation management more generally (Lindenmayer and Likens 2010, Sutherland and Wordley 2017). This leads to uncertainty in what action to take and in how effective a given investment in that action might be. Faced with costly management options and uncertain returns, economic techniques such as return on investment (ROI) analysis can be useful for decision makers (Murdoch et al. 2007).

Few studies have linked the costs of lethal control of overabundant native species with changes in their abundance. Several studies have used ROI and associated cost-effectiveness analyses for invasive species management questions such as evaluating the relative effectiveness of alternative control actions (Nugent and Choquenot 2004) or modelling the cost of achieving progressively lower targets for invasive species populations (Krull et al. 2016). We urgently need a similar level of attention on overabundant species given that, in some cases, they outnumber invasive species as threats to other native species. For example, globally, ten native bird species are threatened by an introduced bird species, but 15 native bird species of conservation concern are affected by other native birds through hybridisation, 22 through brood parasitism, 58 through competition, and 99 by predation (Baker et al. 2014). In Australia, competition or predation from 18 native birds is considered a threatening process for 20 IUCN-listed threatened or near-threatened birds (Garnett et al. 2011), whereas only 16 introduced species have been recognised as threats to these birds.

Here, we assess an experimental culling program aimed at reducing the population of an overabundant native bird, the noisy miner (Manorina

melanocephala), whose aggressive competitive behavior is listed as a Key Threatening Process under Australian biodiversity conservation legislation due to its impacts on endangered small woodland birds (Department of the Environment 2014). The endemic colonial honeyeater genus, *Manorina*, is foremost among the threats represented by overabundant native birds in Australia. Three of the four species in the genus have become overabundant since European settlement and have negative impacts on other native birds due to extreme interference competition (Mac Nally et al. 2012, Leseberg et al. 2014, Kutt et al. 2016). The noisy miner is particularly problematic because of its hyper-aggressive competitive behavior and unique effectiveness in structuring avian assemblages at a sub-continental scale in remnant woodland habitat in heavily-cleared agricultural landscapes (Dow 1977, Maron et al. 2013). Some ecologists advocate culling as the only response that could be practically instituted in time to prevent further declines and possible extinctions of small woodland birds already threatened by habitat modification (Clarke and Grey 2010, Thomson et al. 2015, Mortelliti et al. 2016). Localised culling and translocation have been used to manage populations of two other Manorina species, the bell miner (M. melanophrys) (Clarke and Schedvin 1999) and the yellowthroated miner (M. flavigula) (O'Loughlin et al. 2017). Both studies reported limited success, with recolonization occurring soon after the cull. In two of the four published studies on culls or translocations of noisy miners, average reductions in noisy miner abundance of between 35% and 71% in the twelve to sixteen months following removal were achieved (Grey et al. 1997, Grey et al. 1998). In a recent experimental cull, no such reduction in abundance was seen due to rapid recolonization (Davitt et al. 2018). The reasons for the variability in effects are unclear and, as Grey's studies used only three and four replicates respectively, broader inference to other systems is limited. In another study, ongoing unofficial culling combined with revegetation prevented establishment of new colonies but the experimental site was not controlled or replicated and the revegetation confounded the results of the cull (Debus 2008). No cost analysis was done in the Debus or Davitt studies, and although costs were reported for the first two studies (Clarke and Grey 2010), costs were not related to effectiveness of the action. In our study, we set an objective of reducing noisy miner abundance through culling to below 0.6 - 0.8birds/ha, the impact threshold above which noisy miners structure woodland bird species assemblages (Mac Nally et al. 2012, Thomson et al. 2015). We aimed to investigate the relationship between culling effort and reduction in abundance of noisy miners in the 12 months following the cull by addressing the following questions:

Is culling an effective tool to reduce the abundance of noisy miners in remnant woodland patches in the short term?

Past observational studies of home range (Dow 1979) combined with expert elicitation and evidence from previous removals (Grey et al. 1997, Grey et al. 1998) suggested that recolonization by noisy miners is not an obstacle to success. We therefore predicted that treatment sites would have lower mean noisy miner abundance after the cull than control sites.

How much culling effort is required to remove noisy miners from remnant woodland patches?

We estimated the number of person-hours (excluding travel time) and the total, per-bird and per hectare costs of the cull. In a published study of a previous noisy miner cull, costs of AU\$17 (2017 prices) per bird were reported and 5 birds were culled per person-hour (Clarke and Grey 2010). We predicted that our effort and costs would be in a similar range.

Does greater culling effort result in a greater reduction in noisy miner abundance?

To achieve a particular target abundance, managers need to know if there is a direct relationship between culling effort and post-cull abundance of overabundant species. We completed an ROI analysis to assess whether increased effort led to greater declines in noisy miner abundance. Given that all sites were very open woodland with minimal understorey and good visibility (Figure S1), we expected effort required per bird culled to be similar across sites and that the principal determinant of total effort expended per site would be patch area. We predicted that treatment sites where greater total culling effort was expended would have a greater change in absolute noisy miner abundance to zero in all treatment sites, we predicted that the relative change in noisy miner abundance per unit effort would be similar across sites.

We use this case study to illustrate the challenges faced by managers in choosing appropriate management responses to overabundant native animals when knowledge is limited and expensive to obtain, and to show the importance of well-monitored and costed empirical studies to assess the effectiveness of management actions.

2.2 Methods

2.2.1 Study region

The study was conducted from 2015 to 2017 in a total of 208ha of remnant woodland patches over a landscape of 471 km² in the conjunct shires of Gundagai (35°03'55.5"S 148°06'18.7"E) and Junee (34°52'11.7"S, 147°35'07.9"E) in the South West Slopes bioregion of south-eastern Australia (Figure 1).



Figure 1. a) Study region in south-eastern Australia.

Numbers in boxes refer to the seven farms on which treatment and control patches were located. b), c) Maps showing relationship of treatment and control patches, and landscape configuration, on two example farms.b) is Farm 2; c) is Farm 4.

This region has a continental climate with hot dry summers and cold winters, with average annual rainfall 624mm (Gundagai) and 526mm (Junee) (Bureau of

Meteorology 2017). The region lies within the sheep-wheat belt of New South Wales, a highly fragmented agricultural landscape where more than 85% of the original temperate eucalypt woodland has been cleared with local losses even higher (Lindenmayer et al. 2005, Benson 2008). The majority of remnant woodland in the bioregion is on private land with 2.28 per cent of the total land area under conservation tenures (Office of Environment and Heritage 2015). Woodland is primarily box-gum grassy woodland dominated by white box (*Eucalyptus albens*), grey box (*E. macrocarpa*), yellow box (*E. melliodora*), Blakely's red gum (*E. Blakelyi*) and some mugga ironbark (*E. sideroxylon*). Box-gum grassy woodland is a critically endangered ecological community with local losses in extent as high as 98% (Threatened Species Scientific Committee 2006) . Remnant patches suffer degradation from multiple exogenous disturbances including grazing by cattle and sheep, weeds, invasive species, removal of coarse woody debris and changed nutrient and hydrological regimes (Prober and Thiele 1995).

2.2.2 Experimental design

We selected seven mixed arable/grazing farms in the study region, based on presence of remnant woodland patches, landholder engagement and willingness to participate in the study. We established eight replicate pairs of experimental treatment and control patches on these farms (six farms had one replicate pair, one farm had two). We randomly allocated patches in each of the eight replicates to treatment or control.

The two patches in each pair were matched by size and vegetation characteristics. Patches ranged from four to 49 ha (mean = 13ha). Study patches were in a generally homogeneous agricultural landscape and were broadly similar in tree species, tree density, absence of shrub layer and extent of surrounding woodland. Patches in a treatment/control pair were at least 1142m apart (mean = 2224m, maximum = 6405m) to ensure spatial independence and discourage recolonization following the cull. This was based on Dow's (1979) indication of a maximum noisy miner home range of about 212m. Based on our belief that a coherent social connection between coteries of noisy miners could not be maintained across hundreds of metres of agricultural land, we assumed that colonies did not extend across more than one patch.

Each farm was considered a coherent ecological unit within which management of woodland patches was assumed to be the same (Cunningham et al. 2007). Proximity of each pair of patches ensured that surrounding landscape configuration was the same. Previous monitoring of these sites as far back as 2000 indicated that all patches had consistent detection rates of noisy miners of more than 20% (Mortelliti et al. 2016).

2.2.3 Experimental treatment

We culled noisy miners from the eight treatment patches during the nonbreeding season in May and June 2016 to ensure breeding adults were not removed from nests and to avoid disturbance to breeding small woodland birds. Culling was done with a 12-gauge shotgun using number 9 shot and was applied across the whole treatment patch and to a radius of 500m where patches abutted potential sources of recolonization. Noisy miners forage mostly in the open canopy characteristic of many eucalypts. This, combined with the open vegetation structure of study patches, facilitated the cull.

We defined a complete cull as one where all birds in the patch were shot and there was no visual or vocal response from noisy miners to a 45-minute continuous playback of a randomly rotated playback of their calls. Due to the large number of birds present, we visited some sites on consecutive days to complete the cull. We surveyed noisy miner abundance in each site within two days of the cull. We conducted a second complete cull within three weeks of the first to account for the fact that some resident birds may have escaped the original cull. At least two people were present at each cull, the shooter and an assistant. Where an immediate clean kill was not achieved, the assistant retrieved birds and euthanized them using cervical dislocation, which is the recommended method of humane dispatch.

2.2.4 Survey protocols

To ensure standardised experimental monitoring units, we surveyed a randomly located 2ha study site based around a marked 200m transect in each patch. To determine the effect of the cull, surveys were conducted according to a BACI (Before-After-Control-Impact) design, with noisy miner abundance measured in the pre-cull 2015 breeding season and in the post-cull 2016 season. This approach controlled for annual environmental variations across the region. Breeding seasons are variable in Australia, but using our long-term knowledge of the study area (Lindenmayer et al. 2010, Montague-Drake et al. 2011) and published information about latitudinal and environmental influences on bird breeding, we considered the breeding season to be September-January (Morcombe 2003).

We began noisy miner surveys in study sites nine months before the cull and continued for twelve months after. The same observer surveyed noisy miner abundance in all sites nine times before and 22 times after the cull. Surveys consisted of a fifteen-minute walking count of noisy miners up to 50m either side of the 200m

transect in each patch. Noisy miners are medium-sized (Okada et al. 2017), communal and vociferous with high detection rates generally achieved (Mortelliti et al. 2016) but often become less mobile and vocal once the observer stands still. We therefore considered that this moving method achieved more accurate estimates of abundance of noisy miners compared to other survey methods such as point counts. We also considered that this method reduced double counting as in this open country it was generally possible to keep a tally of birds which moved longitudinally along the transect as the observer moved.

Thirteen of the 16 study patches were already in use in the South West Slopes Restoration Study, a long term ecological monitoring program conducted by the Australian National University (Cunningham et al. 2008). The program has conducted annual monitoring of birds in woodland patches since 2000 (Lindenmayer et al. 2016), so noisy miner detection rates were available for those 13 sites over a 16-year period.

2.2.5 Statistical analysis

Our goal was to assess the impact of the culls on noisy miner abundance over time whilst accounting for other factors likely to influence abundance, and to calculate the costs and effort of any reduction in abundance achieved.

2.2.5.1 Is culling an effective tool to reduce the abundance of noisy miners in remnant woodland patches in the short term?

To answer this question, we fitted generalised linear mixed effects models (GLMMs) to noisy miner abundance using first a Poisson distribution and then a negative binomial distribution, both with logarithmic link functions (Zuur et al. 2009). Akaike Information Criterion (AIC) scores were lower when we used a negative binomial distribution, indicating overdispersion of data. We modelled the response across the full time series of the study (September 2015 - May 2017) to quantify how the cull affected noisy miner abundance with elapsed time since the cull. We expected the biggest effect of the cull on noisy miner abundance in the period immediately following the cull before potential recolonisation. We also were interested to see if this effect lasted until the breeding season following the cull as one aim of reducing noisy miner abundance is to make remnant patches dominated by noisy miners available to small woodland birds for breeding. We therefore ran additional models on subsets of the full series to see if there was any difference in the abundance response in the period immediately before and after the cull (April -September 2016) and in the pre- and post-cull breeding seasons (October - December 2015, October - December 2016).

We first ran a base model with phase (binary: before cull/after cull), treatment (binary: control/treatment) and treatment:phase interaction. We then ran further models including season where applicable (binary: breeding/non-breeding), and the following patch characteristics which we expected to influence noisy miner abundance: a) Patch area; we expected larger patches to support larger populations of noisy miners in the 2ha experimental unit due to larger resource concentrations in these patches (Connor et al. 2000); (b) Productivity; noisy miners favor productive sites, so we used Topographic Wetness Index (TWI), sensu Montague-Drake et al. (2011), as a proxy for productivity; (c) Tree stem density; we used the average of the number of tree stems counted in a 20m x 20m quadrat at each of the three marker posts along the 200m site transect in each patch. Noisy miners favor open woodland rather than denser forests but also inhabit mixed woodland where eucalypt stem density is above 5/ha (Maron 2007). All the sites in this study were open eucalypt woodland with low density of tree stems (mean = 5.1/ha, SD = 4.0), but based on previous studies we assumed that sites with lower stem density would have higher noisy miner abundance (Howes et al. 2010); (d) Percent tree cover within 100ha and 1000ha of site transects; noisy miner abundance in patches is lower in landscapes with higher tree cover (Montague-Drake et al. 2011).

We included Farm as a random effect to account for inherent differences in historical and current management between the farms on which the paired treatment/control sites were located. Site was a random effect to account for inherent differences between sites within each replicate. We selected models based on lowest AIC score combined with parsimony of predictor variables (Burnham and Anderson 2003). We checked standard diagnostics to ensure model assumptions were not violated.

The key element of a BACI design is the interaction between treatment and phase, specifically, how much the treatment group changed between phases relative to how much the control group changed over the same time period. The model coefficients are on the natural log scale. We report results on the back-transformed scale to give expected numbers of noisy miners (holding other model variables at their mean values). 95% confidence intervals are also reported (See Appendix S1 for fuller explanation of this methodology).

2.2.5.2 How much culling effort is required to remove noisy miners from remnant woodland patches?

To measure direct effort expended in the cull, we used person-hours of labor. We excluded travel time to eliminate biases due to spatial arrangement of sites. We estimated per-site, per hectare, per bird and total costs of the cull by calculating costs
of travel, labor and materials. Labor was costed at AU\$50 per hour based on standard rates for technical staff involved in this study. Commercial costs of shooting are very similar (Professional Shooting Services Pty. Ltd, pers. comm.).

2.2.5.3 Does greater culling effort result in a greater reduction in noisy miner abundance?

We combined results from the first and second questions in a return on investment analysis (Auerbach et al. 2014). We defined ROI as the percent reduction in noisy miner abundance per unit of effort. We evaluated whether treatment sites that received more culling effort had better outcomes in terms of declines in noisy miner abundance. Additionally, we used a GLMM with a negative binomial distribution and log link function to test the response of noisy miner abundance to culling effort in treatment sites. We measured effort as person-hours standardized by patch area and we used farm as a random effect.

2.3 Results

The mean sum of noisy miner abundance in treatment sites before the cull was 510. We removed a total of 538 noisy miners from the treatment patches and buffer areas over the two culls. The mean sum of noisy miner abundance in treatment sites after the cull was 512, indicating net immigration. The average number of birds culled was 5.6/ha (SD = 3.9). We achieved a clean kill rate of 86%. The maximum number of birds culled in a patch was 131 (patch size = 19.9ha) and the minimum was 36 (patch size = 16.9ha). Noisy miner abundance was highly variable in time and space and was greater during the winter non-breeding season than the summer breeding season (Figure 2). Mean abundance per 2ha site was lowest in post-cull treatment sites (mean = 5.8, SD = 5.3), and highest in post-cull control sites (mean = 7.1, SD = 5.9).

2.3.1 Is culling an effective tool to reduce the abundance of noisy miners in remnant woodland patches in the short term?

The most parsimonious model contained patch area, treatment, phase, treatment:phase interaction and season (Table 1, Table S2). In our best models, expected noisy miner abundance was lower in treatment sites post-cull than pre-cull. Over the whole period of the study (up to 370 days after the second cull), modelled post-cull changes in noisy miner abundance (with 95% confidence intervals) were 4% (-12%, 23%) for control sites and -22% (-35%, -8%) for treatment sites (Figure 3 (a)).



Figure 2. Plot of noisy miner abundance over the period of the study.

Each point represents one site survey. The fitted curves show the trajectory, with 95% confidence intervals, of noisy miner abundance. The dotted vertical line indicates the time of the final cull (May - June 2016). The red point at zero abundance at the bottom of this line indicates the zero count of noisy miners in all treatment sites immediately after the cull. No survey was conducted in control sites at this time.

When we compared pre- and post-cull breeding seasons (up to 251 days postcull), noisy miner abundance in control sites increased by 21% (-0.3%, 47%) and declined by 13% (29%, -6%) in treatment sites. For the period immediately before and up to four months after the cull (up to 120 days post-cull) abundance declined by 15% (39%, -18%) in control sites and by 24% (44%, -6%) in treatment sites (See Appendix S1, Table S1, for full details of best models for the three time periods). In both control and treatment sites before and after culling, noisy miner abundance remained higher than the threshold of 0.6 - 0.8 birds/ha above which noisy miners structure species assemblages (Mac Nally et al. 2012, Thomson et al. 2015).

Season had a bigger effect on noisy miner abundance than treatment (Table 1). Expected noisy miner abundance during the non-breeding season was 53% (37%, 71%) higher than during the breeding season. The effect of the cull (represented by the treatment:phase interaction) was to reduce the expected noisy miner abundance by 25% (5%, 41%).

Table 1. Model parameters used in final model as predictors of noisy miner abundance (Whole period of study: N=496 observations in 16 sites), showing the effect size (coefficient estimate) and uncertainty (lower and upper 95% confidence intervals) for fixed effects, and the variance explained by random effects.

Fixed effects	Coefficient estimate (back- transformed)	Lower confidence interval	Upper confidence interval
Intercept	4.89	3.64	6.59
Treatment (Cull)	1.05	0.70	1.59
Phase (post-cull)	1.04	0.88	1.23
Season (non- breeding)	1.53	1.37	1.71
Log scaled area	1.33	1.04	1.71
Treatment:Phase	0.75	0.59	0.95
Random effects	Variance (log scale	2)	
Farm	0.01		
Site	0.14		

The relative change in noisy miner abundance (calculated as abundance after cull divided by abundance before cull) was greater in treatment sites than in control sites (Figure 3(b)). We divided the relative change in abundance for the treatment sites by the corresponding quantity in the control sites, which we label as our relative treatment effect (Figure 3(b), rightmost plot). A full list of models with AIC scores is provided in the Appendix S1, Table S2

2.3.2 How much culling effort is required to remove noisy miners from remnant woodland patches?

The two culls completed in treatment sites cost a total of AU\$13069, labor accounting for 91% of this (Table 2). This is an average of \$24 per bird (+/- \$6) or \$136 per ha of patch cleared (+/- \$17). All noisy miners using treatment sites at the time of the cull were removed. The average number of birds removed per personhour of culling effort was 2.9 (range 1.5 - 4.3). More birds were culled in larger sites (r (8 treatment sites, 6 degrees of freedom) = 0.60, p = 0.12). Effort and patch area



Figure 3. (a) Expected noisy miner abundances over full period of study according to the best model, with 95% confidence intervals.

The dotted line at 1.2 birds/2ha is the impact threshold of noisy miner abundance on species assemblages (Thomson et al 2015). (b) Relative differences in expected noisy miner abundance before and after the cull in treatment and control sites respectively, with 95% confidence intervals. The dotted line at 1.0 represents a ratio of 1 i.e. no difference between the expected abundances. Rightmost plot is the relative difference in the differences between treatment and control shown in the previous two plots.

Table 2. Total costs of the noisy miner cull partitioned into

labor costs, travel costs and perishables (ammunition). Costs are given in Australian dollars.

Expense	AU \$
Labor (cull) 212 person-hrs @ \$50 per hour	9700
Labor (travel) 43 person- hrs @ \$50 per hour	2150
Labor (Total)	11850
Travel (980km @ \$0.75/km)	735
Ammunition (approx. 1100 rounds @ \$220 per 500)	484
Total cost	13069

were therefore correlated (r = 0.69, p = 0.06) as were effort and number of birds culled (r = 0.85, p = 0.01). There was little correlation between effort and number of birds culled/ha (r = -0.24, p = 0.56) suggesting that effort had similar output across the different patch sizes (see Appendix S1, Figure S2, for details of relationship between effort, patch area and number of birds culled).

2.3.3 Does greater culling effort result in a greater reduction in noisy miner abundance?

Relating the relative change in mean noisy miner abundance in each patch to culling effort showed variable ROI which was not due simply to differences in patch area (Figure S3). In our GLMM relating the response of noisy miner abundance in treatment sites to effort, effect size for a given change in effort is represented by the coefficient estimate for the effort:phase interaction multiplied by the magnitude of the change in effort. Confidence intervals for the effort:phase coefficient estimates for all time periods modelled overlap zero (Table S3).

2.4 Discussion

We completed a controlled, replicated and rigorously monitored experimental test of the efficacy of a cull as a means of reducing abundance of an overabundant native animal. By calculating the costs of the intervention at a patch- and landscapescale, we related management effort to the change in abundance of the species and assessed return on investment. Our study species was an overabundant native Australian bird whose extreme aggression in the highly modified agricultural landscapes of eastern Australia has had significant impacts on avian species assemblages on a sub-continental scale (Mac Nally et al. 2012, Maron et al. 2013). We formulated hypotheses about the likely response of the species to culling based on existing knowledge of the ecology of the species. Unexpectedly, we found that noisy miners recolonized sites immediately after each cull (Figure 2) and that postcull change in abundance was not significantly related to culling effort. This outcome suggests that culling may not always be an effective management action for controlling populations of overabundant species in highly modified agricultural landscapes even in the short term. In the remainder of this paper, we further discuss the key outcomes of our experiment in relation to our three research questions and comment on the implications of our findings for management of overabundant native species when outcomes are uncertain.

2.4.1 Is culling an effective tool to reduce the abundance of noisy miners in remnant woodland patches in the short term?

The cull achieved a mean 22% reduction in noisy miner population in treatment sites compared to a 4% increase in control sites. However, due to immediate recolonization, mean abundance in treatment and control sites before and after the cull remained 3-5 times higher than published impact thresholds (Figure 3(a)) (Mac Nally et al. 2012, Thomson et al. 2015). As the management objective was to reduce

noisy miner abundance to the point at which their numbers no longer impact small woodland birds, the cull was, therefore, a failure.

Immediate recolonization was unexpected based on our understanding of the species' small home range and sedentary habit (Dow 1979), expert elicitation regarding the species' response to culling (M. Maron, pers. comm.), and prior experimental results (Grey et al. 1997, Grey et al. 1998). However, a recent experimental cull with more replicates and in bigger sites than the work by Grey, also recorded rapid recolonization (Davitt et al. 2018). Where the recolonizing birds came from remains unclear. The congeneric bell miner has two recolonizing strategies, involving either relocation of complete colonies or dispersal of parts of colonies (Dare et al. 2008). We do not have sufficient evidence from this study to show if these strategies apply to noisy miners, but there are two possible explanations for our findings: i) In this highly fragmented landscape, the species has a larger home range than expected from studies in the northern extent of the species' range (Dow 1979). Bioregional differences have been reported in other aspects of the species' behavioral ecology (Thomson et al. 2015). A larger home range implies that colonies extend across more than one woodland patch. Hence, members of a colony residing in one patch have moved into a different patch within the same colony; ii) Birds have moved in from an adjacent colony or colonies. Explanation ii) may indicate a "vacuum effect" (Carter et al. 2007) whereby birds move into the patch when it is vacated by culling because it provided some advantage, such as more concentrated resources. Ecological release mechanisms (sensu Kohn 1972) such as "vacuum effects" following removal of overabundant natives or exotic invasive species are reported widely and across taxa (Donnelly et al. 2003, Treves and Naughton-Treves 2005). We observed increased intraspecific aggression among recolonizing birds following the cull suggesting that they were new to the patch and needed to establish new social relations in the new territory. Such aggression has been reported between translocated birds and existing colonies (Clarke and Schedvin 1997). This does not, however, indicate whether recolonizers came from the same or a different colony. Not all individuals in a colony will have had contact with all others so recolonizers and other colony members might still interact aggressively (Higgins et al. 2001).

Noisy miner abundance was spatially variable, particularly in the non-breeding season when the culls were completed. We cannot, therefore, confidently attribute to the culls the initial increases in abundance seen in some sites in the immediate post-cull period (Figure 2). Such an effect, however, has been observed in other birds where "floating individuals" without a fixed territory rapidly recolonize vacated habitat because they were already familiar with the territory and are able to determine when it becomes available (Bruinzeel and Van de Pol 2004). Noisy miner colonies

can include marginal habitat with low tree density in agricultural landscapes (Grey et al. 2011) so it may be that such birds take advantage of an open niche when higher value woodland patches are cleared of resident birds.

Release mechanisms are a major obstacle to the successful use of culling as a measure to reduce abundance of overabundant native animals. They mean that if we wish to reduce abundance permanently through removal, we need to continue removing animals at a level greater than demographic compensation through immigration or reproduction. This increases the cost of culling, a particular issue given the large spatial scale over which many overabundant native species exert their effects (Livezey 2010, Maron et al. 2013, Lieury et al. 2015). Species such as the noisy miner, with highly complex social relations (Dow 1970), may also exhibit demographic compensation mechanisms, such as increased reproduction or juvenile survival, as a result of social disruption following culling. Negative impacts on species of conservation concern due to such disruption have been reported in several species (Carter et al. 2007, King et al. 2011).

Our experience of the failure of patch-scale culling to reduce abundance of an overabundant native species highlights the importance of being able to answer critical questions about the ecology of the species. Before expending scarce conservation resources on potentially ineffective management actions, we need accurate ecological knowledge of the species, including its home range and population regulation mechanisms (Kierepka et al. 2017). For social species like the noisy miner, we need, in addition, an understanding of the spatial extent of colonies in relation to woodland patches and the conditions under which individuals or colonies recolonise culled areas. Vegetation configuration at patch and landscape scale is likely to have an impact on the effectiveness of culling overabundant native species whose overabundance has been mediated by habitat modification (Clarke and Grey 2010, Foster et al. 2014). In addition, therefore, we need an understanding of how culling interacts with vegetation configuration. Four noisy miner culling programs have been reported on over the last two decades (Grey et al. 1997, Grey et al. 1998, Debus 2008, Davitt et al. 2018) but at least six others have been undertaken in the same period, at different scales and with varying levels of success. The influence of local differences in vegetation configuration on the responses of metapopulations to culling makes broad inference from localised culls difficult. There is an urgent need, therefore, to synthesise existing knowledge to determine under what circumstances culling is most likely to be successful.

Our experiment aimed to show the effects of culls at a tractable and manageable patch-scale. We acknowledge that culling at a larger scale (such as farm or district) would likely slow the rate of recolonisation. Patches might then remain free of noisy miners long enough for small woodland birds to move back in. Short of a landscapescale elimination of the species, however, with its own uncertainties about the potential for unexpected ecological outcomes, even farm-scale culling is likely to be eventually overcome by recolonisation from further afield since farms have porous boundaries.

The fundamental unknown here is what promotes noisy miners to leave their home range and recolonise another site following a cull. One suggestion has been to cull only the inner core of a colony (Maron, M, pers. comm.) such that remaining birds on the outside of the colony prevent recolonization by birds from other colonies. This is only applicable to larger patches of woodland where a core of birds can be identified and removed. An alternative strategy might be removal of selected colonies in a patchwork manner, the implication being that removing a whole colony, rather than just part of a colony, as we may have done in this patch-scale cull, is less likely to result in recolonization. This might be a good approach in high value biodiversity areas surrounded by more intact areas with fewer sources of recolonization. It has been suggested, however, that removing whole colonies fosters recolonization whereas leaving parts of a colony intact maintains territoriality and therefore discourages recolonization (Davitt et al. 2018).

2.4.2 How much culling effort is required to remove noisy miners from remnant woodland patches?

Global estimates of the costs of controlling overabundant native birds to protect threatened birds range from US\$14 to US\$2800 per bird (Livezey 2010). The costs expended on the cull in this study (AU\$24 per bird) were at the lower end of this range but of the same order of magnitude as the previous experimental culls of the species (Clarke and Grey 2010). In spite of this expenditure, however, we failed to reach the objective of reducing noisy miner abundance below published impact thresholds. Measuring costs per individual culled does not account for the temporal and spatial scale over which a patch-scale cull would need to be completed to achieve ecological goals (Saunders et al. 2010, Lieury et al. 2015). In this regard, the noisy miner is particularly problematic given that its ecological impacts occur over more than one million km^2 (Maron et al. 2013), an indication of the extreme habitat modification that has occurred in eastern Australia in the two centuries since European settlement (Hobbs and Hopkins 1990). Assuming a conservative average density of 3 birds per hectare to account for the fact that vegetation supporting noisy miners is not present across the whole of this range (we recorded densities above 20 per ha on occasions (Figure 2)), this would mean a minimum of thirty million birds and a direct labor cost of AU\$720 000 000 (excluding travel and materials costs) to

reduce the abundance of noisy miners across their whole range. The cost of this kind of program suggests that it would be wise to properly assess and compare (e.g. using ROI) the benefits and costs of alternative management programs such as appropriate revegetation, which is known to deter noisy miner colonization (Grey et al. 2011, Lindenmayer et al. 2018). It is difficult to provide globally applicable costs of revegetation, but in the agricultural landscapes of this study, total public costs for whole-of-paddock-restoration for a 20ha project over ten years have been estimated at AU\$2580/ha (Ansell et al. 2016). Whilst this is almost eighteen times the per hectare cost of our (largely ineffective) culling, the likelihood of successful ecological outcomes may be much greater as noisy miners have been shown to avoid restoration plantings (Lindenmayer et al. 2016, Mortelliti et al. 2016).

2.4.3 Does greater culling effort result in a greater reduction in noisy miner population?

Our *a priori* prediction that more effort would result in a greater absolute reduction in noisy miner abundance was proved wrong because post-cull abundance was not a function of culling effort. Rather it was due to recolonization. As a result, there was no overall return on investment, particularly given that noisy miner abundance remained above ecological impact thresholds (Figure S3; Table S3).

2.4.4 Culling, uncertainty and ecological risks: A general framework for planning responses to overabundant species

We have shown that it is not straightforward to predict the outcomes of a cull of an overabundant native species, and that the effectiveness of control efforts and the duration of results can be highly variable. This creates uncertainty in management planning. If management is to be effective and lasting, and if we are to pre-empt potential problems, we need to prioritize actions according to best practice, cost-effective management guidelines. Adaptive responses to experimental management programs are appropriate to resolve the greatest uncertainties hindering decisions about which action to apply or when to apply it (Tulloch et al. 2017). Critical ecological and management uncertainties for overabundant species include: i) The relationship between the abundance of the overabundant species and its ecological impacts (Lieury et al. 2015). In conjunction with effective monitoring, this informs which sites are most critical for management; ii) The relationship between conservation effort expended and population reduction of the overabundant species. This shows the direct impacts of management (Kubasiewicz et al. 2016) and informs how much management we need to do; iii) The ecological factors, such as potential for ecological release, the species' home range, and the species' population ecology, that control recolonization by the overabundant species (Lieury et al. 2015, Kierepka et al. 2017). This informs how to monitor the management action; iv) The ecological factors controlling recovery of species of conservation concern through recolonization or local population growth. This informs whether and how we monitor species of conservation concern. A key additional element of our study is the effect of the cull on occurrence and behavior of small woodland birds impacted by noisy miners. This will be reported elsewhere but we offer preliminary findings here. The limited decline in noisy miner abundance achieved in treatment sites led to small increases in rates of detection and foraging of small woodland birds but no change in artificial nest predation rates; v) The possibility of a management action making things worse (Donnelly et al. 2003, Walsh et al. 2012, Lazenby et al. 2015). This informs whether we need to scope alternative actions or alter management to avoid or diminish potential perverse outcomes; vi) other management actions that might, instead of or as well as a cull, achieve better outcomes (Tulloch et al. 2016).

2.4.5 Conclusions

Our study demonstrates the importance of empirical evidence and knowledge of likely costs before intuitively attractive, but not necessarily ecologically effective, culling programs are applied more broadly for the control of overabundant native animals. Costs are a particular issue where recolonisation necessitates ongoing culling. The size, range and mobility of noisy miner populations present particular challenges for management (Thomson et al. 2015) and their impacts are likely to get worse under climate change (Bennett et al. 2015). Deforestation continues in many parts of the world (FAO 2015) and has increased in eastern Australia in recent years (Evans 2016). Where this results in fragmentation and increased edge habitat, it is likely creating new opportunities for overabundant native species such as noisy miners to impact vulnerable ecological communities. Management of overabundant animals requires strategic experiments such as this study to ensure that the most efficient and effective options for native species recovery are discovered and delivered. In the absence of empirical knowledge, we cannot assume a patch-scale cull of an overabundant native animal will reduce its abundance, let alone achieve flow-on benefits for species of conservation concern.

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Appendix S1



Figure S1. Typical study site

Calculating expected noisy miner abundance Regression equation for best model (ignoring random effects):

Ln expected nois	y miner abunda	ance = $\beta_0 + \beta_1$ Treatment	+ β_2 Phase +
β ₃ Season	+	β_4	Area
+ β_5 Treatment:Phase			

Using addition of logs, expected ln noisy miner abundance for phase, treatment and phase:treatment interaction, assuming constant (ie mean) area and constant season (non-breeding) is:

	Control	Treatment
Phase 0 (before cull)	(β ₀)	$(\beta_0 + \beta_1)$
Phase 1 (after cull)	$(\beta_0 + \beta_2)$	$(\beta_0 + \beta_1 + \beta_2 + \beta_5)$

To calculate the Treatment: Phase effect:

 Calculate relative change in expected noisy miner abundance before and after the cull in treatment and control sites respectively:
 Relative change in expected noisy miner abundance =

Expected abundance after cull Expected abundance before cull ii. Calculate the relative difference between the change in expected abundance in treatment and control sites to show effect of treatment:phase interaction:

Relative difference between change in expected noisy miner abundance in

treatment and control sites

 $= \frac{\frac{Expected abundance after cull}{Expected abundance before cull} (Treatment)}{\frac{Expected abundance after cull}{Expected abundance before cull} (Control)}$

$$= \frac{\frac{\exp\left(\beta_0+\beta_1+\beta_2+\beta_5\right)}{\exp\left(\beta_0+\beta_2\right)}}{\frac{\exp\left(\beta_0+\beta_1\right)}{\exp\left(\beta_0\right)}} =$$

 $\exp(\beta_5)$

Worked example

(using dataset for whole period of study, best model:

Model output:

Predictor	Coefficient
	estimate
Intercept	1.59
Treatment	0.05
Phase	0.04
Treatment:phase	-0.29

Ratio of change in expected noisy miner abundance in treatment sites to change in abundance in control sites:

Exp(-0.29) = 0.75

Calculating ln expected noisy miner abundances by treatment and phase using addition of logs (with backtransformed values in brackets)

	Control	Treatment
Phase 0 (before cull)	1.59 (4.90)	1.59 + 0.05 = 1.64 (5.16)
Phase 1	1.59 + 0.04 = 1.63	1.59 + 0.05 + 0.04 - 0.29 =
(after cull)	(5.10)	1.39 (4.01)

Table S1. Output summaries for best model with 95% confidence intervals.

Note i) due to the model's log link function, original model output gives coefficient estimates for the log of the dependent variable. The values given in this table have been back-transformed (see worked example above); ii) Coefficient estimates represent the relative change in the dependent variable (expected noisy miner abundance) for a unit change in the corresponding explanatory variable; iii) Area was standardised then logged. Hence the coefficient estimates for area represent the change in expected noisy miner abundance for a unit change in the log of the standard deviation of area.

	Whole period o	of study		Pre- and post-cull breeding seasons		Immediately before to four months after			
	(N=496 observ	ations in 16 si	ites)	(N=256 observations in 16 sites)			cull (N=126 observations in 16 sites)		
Fixed	Coefficient	Lower	Upper	Coefficient	Lower	Upper	Coefficient	Lower	Upper
effects	estimate	confidence	confidence	estimate	confidence	confidence	estimate	confidence	confidence
(back-		interval	interval		interval	interval		interval	interval
transformed)									
Intercept	4.89	3.64	6.59	4.49	3.58	5.63	9.34	6.18	14.13
Treatment	1.05	0.70	1.59	1.10	0.81	1.48	1.01	0.56	1.82
Phase	1.04	0.88	1.23	1.21	1.00	1.47	0.85	0.62	1.18
Season	1.54	1.37	1.73						
Area	1.33	1.05	1.70	1.20	0.98	1.48	1.43	1.13	1.81
Treatment x	0.75	0.59	0.95	0.72	0.54	0.95	0.89	0.56	1.41
Phase									
Randomeffects(logscale)	Variance			Variance			Variance		
Farm	0.01			0.01			1.09 x 10 ⁻⁸		
Site	0.14			0.05			0.02		

Model summaries

Table S2. Summary of all models, in ascending order of AIC score. Note: i) base model used treatment, phase and treatment:phase interaction; the other models were the base model plus the corresponding variable; null models used random effects only; ii) best model for whole period of study was base model plus season and area, AIC = 2640.4

Model	AIC	ΔΑΙΟ
Season	2643.6	0
Area	2689.1	45.5
Null	2691.6	48.0
Base	2692.3	48.7
Tree cover (100ha)	2692.8	49.2
Tree cover		
(1000ha)	2693.0	49.4
Tree stem density	2694.1	50.5
TWI	2694.2	50.6

a) Whole period of study

b) Breeding seasons only

model	AIC	ΔΑΙΟ
Area	1260.9	0
Base	1262.7	1.8
Null	1262.7	1.8
Tree stem density	1263.9	3.0
TWI	1264.1	3.2
Tree cover (100ha)	1264.6	3.7
Tree cover		
(1000ha)	1264.6	3.7

c) Immediately before to 4 months after cull

model	AIC	ΔΑΙC
Area	788.3	0
Null	790.8	2.5
Tree cover (100ha)	791.6	3.2
Tree cover		
(1000ha)	791.9	3.7
Base	792.9	4.6
Tree stem density	794.9	6.6
TWI	794.9	6.6



Figure S2. Relationships between effort, area and number of birds culled



Figure S3. Patch area and return on investment (per cent reduction in noisy miner abundance per person-hour effort) for each of the 8 treatment sites.

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Table S3. Model parameters used in cost model as
predictors of noisy miner abundance in
treatment sites (log scale)

Fixed	Coefficient	Lower	Upper	
effects	estimate	confidence	confidence	
		Interval	interval	
Intercept	1.65	-0.93	1.03	
Effort/Area	0.05	-0.33	0.41	
Phase	0.04	-0.55	0.39	
Effort x Phase	-0.08	-0.18	0.18	
Random	Variance			
effects				
Farm	0.29			

a) Whole period of study (N=248 observations)

b) 2015 and 2016 breeding seasons (N=128 observations)

Fixed effects	Coefficient estimate	Lower confidence interval	Upper confidence interval
Intercept	1.51	0.82	2.20
Effort/Area	0.03	-0.22	0.28
Phase	0.11	-0.40	0.62
Effort x Phase	-0.11	-0.31	0.09
Random	Variance		
effects	0.12		
Farm	0.12		

c) Immediately before to 4 months after cull (N=64 observations)

Fixed effects	Coefficient estimate	Lower confidence interval	Upper confidence interval
Intercept	2.10	0.88	3.32
Effort/Area	0.07	-0.40	0.54
Phase	-0.03	-0.99	0.93
Effort x Phase	-0.11	-0.48	0.26
Random	Variance		
effects Farm	0.28		

Chapter 3: An empirical test of the mechanistic underpinnings of interference competition

Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with https://policies.anu.edu.au/ppl/document/ANUP_003405

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multiauthor papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

Title: An empirical test of the mechanistic underpinnings of interference competition

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Senior author or collaborating authors endorsement:

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Foreword

Chapter two considered the direct output of the cull, noisy miner abundance. The purpose of managing noisy miner abundance, however, is to improve ecosystem function for declining small woodland birds. In chapters three and four, I consider the outcomes of the experimental cull for small woodland birds. Chapter three is an empirical study of the effect of removing an interference competitor on foraging opportunities for small woodland birds and on the amount of harassment suffered by small woodland birds. In temperate eucalypt woodlands of the southeast of Australia, many aggressive bird species harass other species and this is thought to limit foraging opportunities for small woodland birds. It is important to know if reducing noisy miner abundance improves foraging opportunities and reduces harassment for small woodland birds and that noisy miner aggression is not simply replaced by aggression by other species.

Abstract

Interspecific competition is an essential element of the evolution of species and can strongly influence the abundance and distribution of species. Where competition interacts with anthropogenic habitat modification, this natural ecosystem process can become a threatening process. Understanding the mechanisms behind competition in such cases is essential for the formulation of cost-effective management responses for biodiversity conservation. According to the resource availability hypothesis of competition, interference competition limits access to resources by species vulnerable to aggression and wastes energy in evasive responses. Studying competition is notoriously difficult, however, empirical evidence of the resource availability hypothesis is limited, and there are few published experimental studies showing the effect at larger scales. We present the results of a controlled, replicated empirical study of interference competition at a landscape scale. We removed an aggressive, overabundant bird, Manorina melanocephala, whose interference competition is a threatening process for small woodland birds in the highly modified agricultural landscapes of eastern Australia. We monitored foraging and harassment rates of small woodland birds before and after removal to indicate if levels of interference competition changed. Due to unexpected immediate recolonisation, abundance of *M. melanocephala* in treatment sites declined by only 28% relative to control sites. Twenty-four bird species displayed aggressive behaviour towards other birds and 41 bird species were victims of aggression. M. melanocephala was responsible for 66% of all aggressive interactions. After removal, we recorded a doubling in foraging rate of small woodland birds in treatment compared to control sites. This appears to confirm the resource availability hypothesis of competition. Paradoxically, increased foraging was not accompanied by a decline in harassment. Low detection rates of harassment of small woodland birds, combined with the modest reduction in M. melanocephala abundance, make it difficult to draw firm conclusions about the relationship between rates of harassment and rates of foraging.

Keywords

Interference competition, *Manorina melanocephala*, noisy miner, overabundant native species, cull, population control, foraging, harassment

3.1 Introduction

Interspecific interactions such as competition can be a key determinant of the abundance and distribution of species (Case et al. 1974, Darwin 1859, Elton 1927). Through its effect on resource availability, competition can contribute to niche

contraction for less competitive species (Chase et al. 2002, Doherty et al. 2018, Kunte 2008). Interference competition occurs where there is a high degree of competitive overlap and resources are economically defendable, hence resources are monopolised by one group through aggressive exclusion of competitors (Brian 1956, Case et al. 1974). This form of competition can have a particularly strong influence on species assemblages when anthropogenic biotic or abiotic changes favour aggressive generalist species. Competition can then become a threatening process for declining species, leading to biotic homogenisation (Robertson et al. 2013, Rooney et al. 2007). Anthropogenic habitat modification is a particularly prevalent form of pressure that entails both biotic and abiotic changes and can transform interference competition into a threatening process (Bennett et al. 2015, Diller et al. 2016, Leseberg et al. 2014, Robertson et al. 2013). Here, we consider the effects of an extreme form of interference competition exerted by an overabundant, hyperaggressive native bird. In combination with habitat modification, this competition has led to homogenisation of avian assemblages at a scale of over one million km² (Mac Nally et al. 2012, Maron et al. 2013).

Addressing such threats through habitat restoration is difficult politically and practically (Evans 2016, Hinton et al. 2013, Lindenmayer 2017, Mac Nally 2008). In addition, where biotic and abiotic conditions have been changing in the long term, hysteretic effects mean that removing the primary threat of competition may not ensure reoccupation by declining species (Maron et al. 2013, Suding et al. 2004). This is particularly the case where other competitive species have occupied the niche space vacated by declining species (Doherty et al. 2018, Hinton et al. 2013, Maron et al. 2013). Hence, direct intervention to reduce the abundance of species whose interspecific interactions threaten declining species is a common management response (Diller et al. 2016, Grarock et al. 2014, Kosciuch et al. 2008).

Theory suggests that victims of interference competition have poorer access to resources and waste energy in responding to disturbance (Bechet et al. 2004, Ford 1979, Mac Nally et al. 2005, Moore et al. 2016). If this is the case, then reducing the abundance of the interference competitor should improve resource availability for declining species and reduce the amount of aggression suffered. Studying competition is practically difficult, however, empirical evidence of the resource availability hypothesis is limited, and there are few published experimental studies showing such an effect at larger scales.

We tested the effect of a landscape-scale experimental removal of a hypercompetitive native Australian bird, *M. melanocephala* (noisy miner), on foraging and harassment rates of declining small (<63g) woodland birds. This group

is among the most threatened of Australian birds (Barrett et al. 2007). *M. melanocephala* is a medium-sized honeyeater with a weight of 70 - 80g (Higgins et al. 2001). It is a sedentary, colonial species whose extreme co-operative territorial aggression affects a wide range of small woodland birds (Maron et al. 2013). Aggressive exclusion of birds from potential habitat by *M. melanocephala* is a Key Threatening Process under Australian conservation legislation (Department of the Environment 2014). Impacts occur at *M. melanocephala* densities as low as 0.6 birds/ha (Thomson et al. 2015) and across an area of 1.3 million km² (Higgins et al. 2001). The combination of the scale of their impact and the intensity of the interference competition they exert makes *M. melanocephala* both an environmental problem in urgent need of a solution, and an ideal experimental subject to test the mechanisms underpinning interference competition.

Several ecologists have suggested culling of *M. melanocephala* as a management response in some circumstances (Mortelliti et al. 2016, Thomson et al. 2015). Our study therefore has a theoretical and a practical component. We sought to elucidate the ecological processes underpinning the effect of a hyperaggressive competitor on declining bird species and to evaluate the potential for limiting such competition through lethal control of the hyperaggressive species. We used foraging rates and harassment rates as metrics of the intensity of interference competition. We compared these rates for small woodland birds before and after removal of *M. melanocephala*. We posed two questions:

- 1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?
- 2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?

Based on expert opinion (M. Maron 2016, personal communication) and the evidence of previous removals of *M. melanocephala* (Grey et al. 1997, Grey et al. 1998), we predicted that the cull would result in a significant reduction in *M. melanocephala* abundance in treatment sites compared to control sites. *A priori*, we posited three possible outcomes for small woodland birds.

- i. A decline in harassment rates and an increase in foraging rates, indicating that removing *M. melanocephala* improves resource availability.
- An increase or no change in harassment rates and a decline or no change in foraging rates, indicating compensatory harassment by other bird species when *M. melanocephala* are removed.

 A decline in harassment rates but no change in foraging rates, indicating that harassment by *M. melanocephala* is not the principal source of limited resource availability.

However, due to almost immediate recolonisation of treatment sites by *M*. *melanocephala* after each of two culls, final *M. melanocephala* abundance in treatment sites in the post-cull breeding season was higher than expected. Similar compensatory immigration has been reported in a recent cull of *M. melanocephala* (Davitt et al. 2018) and other taxa (Grarock et al. 2012, Kierepka et al. 2017, King et al. 2011, Lazenby et al. 2015). Overall, *M. melanocephala* abundance in control sites increased by 21% (95% confidence intervals: -0.3%, 47%) and in treatment sites declined by 13% (29%, -6%) (Beggs et al. 2019b). We therefore predicted that any difference in the change in harassment or foraging rates between treatment and control sites would be commensurate with this lower than expected decline in *M. melanocephala* abundance.

We also considered two potential complicating factors. First, *Manorina* species are highly social, with a complex co-operative territorial defence system (Arnold 2000, Clarke et al. 1994, Dow 1970) and possible social associations with other species (Fulton 2008). Behavioural changes resulting from replacement of an existing *Manorina* community with new individuals following a cull are therefore possible and this could influence their interactions with other species (Davitt et al. 2018). Second, *M. melanocephala* are not the only aggressive species present in this landscape. *M. melanocephala* structure species assemblages in the agricultural landscapes in which this study took place, favouring larger, aggressive generalist species (Maron et al. 2013). The study therefore also aimed to discover whether these other aggressive species compensate for any post-cull reduction in harassment by *M. melanocephala*.

3.2 Material and Methods

3.2.1 Study area

We conducted our experiment from 2015 to 2017 in the adjacent shires of Gundagai (35°03'55.5"S 148°06'18.7"E) and Junee (34°52'11.7"S, 147°35'07.9"E), in the South West Slopes Bioregion of New South Wales, Australia (Figure 1). This region is part of eastern Australia's agricultural belt. More than 85% of the original woodland has been cleared in the region with local losses even higher (Lindenmayer et al. 2005). The ecological value of remnant patches of woodland is affected by fragmentation and degradation through grazing and changed nutrient and fire

regimes (Hobbs et al. 1990). 2.28 per cent of the land area of the bioregion is under conservation tenures (OEH 2015). The majority of remnant woodland in the region is on private farmland. Biophysical details of the study region are given in Mortelliti and Lindenmayer (2015).



Figure 1. Study region and experimental design. a) Paired treatment/control study patches on study farms. Numbers in boxes refer to farm number. b), c) Maps showing relationship of treatment and control patches, and landscape configuration, on two representative farms. b) is Farm 2; c) is Farm 4.

The study was located within the South West Slopes Restoration Study, a long-term ecological monitoring program conducted by The Australian National University. As part of this program, annual monitoring of birds has been conducted in woodland patches since 2000. Indications are that many small woodland birds have declined whilst *M. melanocephala* and larger aggressive generalist species have increased their range and abundance (Cunningham et al. 2008, Mortelliti et al. 2016). More recently, *M. melanocephala* abundance appears to be declining in the region (Lindenmayer et al. 2016, Mortelliti et al. 2015).

3.2.2 Experimental design

We selected eight paired patches of remnant or regrowth native eucalypt woodland on seven private mixed arable/grazing farms in the region such that six farms had one pair of patches and one farm had two pairs (Figure 1). Patch size ranged from four to 49ha. Within each patch, we used an existing randomly located 200m marked transect as the central axis of a 2ha study site. We randomly allocated one patch in each pair to treatment or control (Figure 1). Each pair of patches was at least 1142m apart to ensure independence and discourage recolonisation post-cull, based on *M. melanocephala*'s published home range of about 200m (Dow 1979). All sites had consistent detection rates of *M. melanocephala* of more than 20%.

Habitat factors at both site and landscape scales affect presence of small woodland birds (Cunningham et al. 2014a, Montague-Drake et al., 2011, Polyakov et al., 2015). Hence, we chose paired woodland patches based on similar size and vegetation characteristics, using a rapid visual assessment, to account for variance at patch scale. We considered each farm to be a coherent ecological unit with consistent management of woodland patches (Cunningham et al., 2007) and for which the surrounding landscape was largely the same. Mean distance between treatment and control sites was 2224m, (SD = 1710m) so any local variations in productivity due to rainfall were likely to be similar in both treatment and control groups.

We used a BACI (Before-After-Control-Impact) design (Stewart-Oaten et al. 1986) to account for annual variations in environmental conditions that might affect bird behaviour or abundance (Lindenmayer et al. 2011, Tulloch et al. 2016a). We conducted foraging and harassment surveys between October and December in all sites in the pre-cull 2015 breeding season and in the post-cull 2016 season.

3.2.3 Experimental treatment

We conducted the cull of *M. melanocephala* in experimental treatment patches using a shotgun in May and June 2016 during the Southern Hemisphere winter, non-breeding, season. We conducted two complete culls at each treatment site. We culled across the whole of each patch and to a radius of 500m where patches abutted potential sources of recolonization such as other woodland patches. We considered culling complete when there was no visual or auditory response by *M. melanocephala* to a continuous 45-minute playback of a selection

of *M. melanocephala* calls. See Beggs et al. (2019b) for full methodology and costings of the cull.

3.2.4 Survey protocols

We conducted eight one-hour surveys of foraging and harassment rates at each site during the breeding season (September – December) before the cull (2015) and in the breeding season following the cull (2016). Post-cull surveys continued up to six months after the cull. The eight repeat surveys were used to eliminate day effects (Field et al. 2002). The observer followed the 200m transect in each site twice in each direction whilst looking and listening for small woodland birds and aggressive interspecific interactions up to 50m either side of the transect. Detection at 40m is considered to be high in forest environments (Mac Nally et al. 2000, Mac Nally et al. 2005). Given minimal understorey and the open structure of the woodland in our study, we assumed high detection rates of birds up to 50m away.

For foraging surveys, on discovering an individual or group of small woodland birds, the observer paused the timer and watched the bird(s) for foraging activity for up to one minute to avoid bias towards conspicuous behaviours. We recorded each foraging observation, whether of a single bird or a group, as one foraging event and also recorded group size. The timer was then restarted and progress resumed along the transect. For harassment surveys, we recorded any aggressive interspecific interaction and noted the species and number of the aggressor and victim along with location (Ground, Air or Canopy), duration, type of interaction (Chase, Supplant, Harassment, Posturing; see Table S1, Appendix), and the victim's response (Retreat, Leave patch, Hold ground, Fight back). We defined aggressor species as species observed initiating at least one aggressive interaction with another species of bird.

We did not conduct surveys during weather conditions likely to inhibit bird activity or detection, such as strong winds, rain and very high temperatures (O'Connor et al. 1980). We conducted six of the eight annual surveys in the five hours after dawn. Two out of eight were done later in the day with sites surveyed on a rotating basis such that over each season all sites were monitored equally at the different times. Such afternoon surveys have been used on previous studies in eastern Australia (Bennett et al. 2015, Robertson et al. 2014). Most surveys were conducted by the same experienced birdwatcher to minimise observer heterogeneity.

3.2.5 Experimental variables

The aim of the experiment was to explain the impact of the culls of *M*. *melanocephala* on the incidence of interference competition and of foraging by small

woodland birds whilst accounting for the influence of other site or landscape variables that might influence the response variables (Table S2, Appendix). Due to multicollinearity, we excluded woodland extent at 100ha and 10 000ha, using only woodland extent at 1000ha in our models.

3.2.6 General approach to modelling

We constructed generalised linear mixed effects models (GLMMs) of the effects of BACI base variables (Treatment, Phase and Treatment:Phase interaction) and other patch and landscape variables on foraging and harassment rates respectively. Treatment and Phase were binary variables. Treatment had values Treatment (cull) and Control (no cull). Phase had values 0 (pre-cull) and 1 (post-cull). We started with a global model which included BACI base variables plus five landscape- and patch-scale predictor variables (Table S2, Appendix). We used a Poisson distribution for harassment models and a negative binomial distribution for foraging models as these gave the lowest AIC score. Models had a logarithmic link function and we included Site and Farm as random effects to account for repeated surveys over time (Zuur et al. 2009). We conducted standard diagnostic tests to ensure model assumptions were not violated. All modelling was done in the glmmTMB package (Brooks et al. 2017) in statistical software R, version 3.3.2 (R Core Team 2017).

We used R package MuMin (Barton 2018) to assess all possible models using all predictor variables, constrained by inclusion of BACI base variables. Model selection was based on lowest Akaike Information Criterion (AIC) score (Burnham et al. 2003).

The purpose of our modelling was to determine if changes in foraging or harassment rates from the pre-cull phase to the post-cull phase were different in treatment compared to control sites. In the BACI design, any such difference is indicated in the Treatment:Phase interaction term. The link function in our models provided the coefficients of predictor variables on the log scale. For simplicity of interpretation, we plot results back-transformed to the non-log scale to give expected numbers of harassment or foraging events with 95% confidence intervals.

3.2.6.1 Qu1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?

To indicate the amount and direction of aggressive interspecific interactions in this landscape under normal circumstances, we prepared an interaction matrix by cross-tabulating all interactions between aggressor and victim species pre-cull. From this matrix we constructed a chord diagram in R package *Circlize* (Gu et al. 2014) to show visually the relationships between aggressors and victims.

Small woodland birds were victims of harassment in only 41 cases across our two phases and two treatments, thereby limiting our scope for analysis to species level. For the purposes of modelling, we therefore aggregated the total number of harassment events where small woodland birds were victims.

3.2.6.2 Qu2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?

We first modelled the sum of foraging events of all species. The dominant species observed foraging, *Pardalotus striatus* (striated pardalote), accounted for 63% of all foraging events by small woodland birds. We therefore repeated models excluding *P. striatus* to assess the effect of the cull on less common species.

To quantify how foraging rates of different species of small woodland birds responded to the cull of *M. melanocephala*, we completed a multivariate analysis, fitting GLMMs by species for species detected foraging four or more times across the period of the study. We used R package *Boral* as this package is designed for multivariate abundance datasets. It uses Bayesian Markov chain Monte Carlo methods to estimate coefficients of variables and accounts for any correlation between response variables by incorporating possible latent variables due to unmeasured covariates. This allows inference about treatment effects at a community level (Hui 2016). We used a Poisson distribution with log link function, used Farm as a random effect and report model results based on 10 000 iterations of the Bayesian Markov chain Monte Carlo estimation method.

3.3 Results

3.3.1 Qu 1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?

Aggressive interspecific interactions are common in this landscape. Across all sites and both phases of our experiment, we observed a total of 253 aggressive interspecific interactions. The average rate of such interactions per hour per 2ha site in the pre-cull phase was 1.19 in control sites and 0.59 in treatment sites. 24 bird species harassed other species and 43 species were victims of harassment, including the 24 aggressor species (Figure 2, Table S3, Table S4, Appendix). Two of the 43 victim species were mammals, *Antechinus flavipes* (yellow-footed antechinus) and *Vulpes vulpes* (European fox), these two species suffering a total of four harassment

events (Table S3, Appendix). Across all pre-cull surveys, *M. melanocephala* was responsible for 65.7% of harassment events with the next biggest aggressors being *Lichenostomus penicillatus* (white-plumed honeyeater) (7.5%) and *Cracticus tibicen* (Australian magpie) (7.1%) (Table S4, Appendix). Ten of the 41 avian victim species were small woodland birds (Table S3, Appendix). We observed a total of 41 harassment events where small woodland birds were victims and a total of 208 events where other birds were victims (Table S3, Appendix).

We found no evidence of a reduction in the total number of harassment events recorded following the cull, either for models which included all victim species or for models which included only small woodland birds (Figure 3, Table S6, Appendix). For models which included all victim species, the model with lowest AIC score included the base BACI variables plus Topographic Wetness Index and Corrected Perimeter to Area Ratio for woodland patches. However, five other candidate models had an AIC score within two units of this model (Table S8, Appendix), the most parsimonious of these being the base BACI model. Similarly, the best model for small woodland birds included only the BACI base variables (Table S8, Appendix). Table S6 (Appendix) shows coefficient estimates for the best harassment models. We found no evidence of a treatment effect on the amount of harassment by *M. melanocephala* (Table S9, Figure S2, Appendix).

3.3.2 Qu 2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?

We recorded small woodland birds foraging in 180 out of 256 surveys. Across all sites and both phases of our experiment, we observed foraging by 17 species of small woodland bird at an average rate of 4.5 foraging events per hour per 2ha site. *P. striatus* accounted for 3.0 foraging events per hour of this total. For all species other than *P. striatus*, we observed foraging in fewer than 13% of surveys in the precull phase.

To explain the differences between foraging rates of small woodland birds in treatment and control sites following the cull, four candidate models that included the BACI base variables (Treatment, Phase and Treatment:Phase interaction) had AIC scores within two units of each other (Table S10, Appendix). The two most parsimonious of these models each contained six explanatory variables:



Figure 2. Interspecific harassment networks in study sites before the cull (Treatment and Control sites aggregated).

Coloured arcs are labelled with each species that was involved in aggressive interactions either as aggressor, victim or both. Chords of same colour as labelled arc indicate an aggressive interaction perpetrated by the labelled species. Where chords intersect with an arc of different colour, the different coloured arc denotes the victim of aggression. Thickness of chord indicates quantity of interactions. See Table S5, Appendix, for species glossary.

Treatment + Phase + Treatment: Phase + Area + Forest extent at 1000ha + Total stems

Treatment + Phase + Treatment:Phase + Area + Total stems + Topographic Wetness Index

For both of these models, foraging rates increased in the post-cull breeding season in treatment sites (Figure 4a) and the relative increase in treatment sites was greater by a factor of two than in control sites (Figure 4b). Coefficient estimates are given in Table S11 (Appendix).



Figure 3. (a) Expected harassment rate of small woodland birds based on the best model, with 95% confidence intervals. Harassment rate is number of harassment events per 2ha site per hour (b) Ratio of expected harassment rates in control and treatment sites before and after the cull. The dotted line at 1.0 represents a ratio of 1 i.e. no difference between the expected harassment rates in the before and after phase. The rightmost plot is the relative difference in the after/before ratio for Treatment and Control. The best model included only BACI base variables: Treatment, Phase and Treatment:Phase interaction.

For models excluding *P. striatus*, six candidate models had AIC scores within two units of each other (Table S12, Appendix). The two most parsimonious of these were the same as for the models which included all species, reported above. According to these two models, the relative increase in foraging in treatment sites was a factor of 10 greater than in control sites in the post-cull phase (Figure 5). Table S13 (Appendix) shows coefficient estimates for these two models.

Of the ten species of small woodland bird included in our multivariate analysis, *L. penicillatus, Smicrornis brevirostris* (weebill) and *Rhipidura leucophrys* (willie wagtail) showed a significant increase in foraging rate in treatment compared to control sites following the cull (Figure 6). None of the remaining species showed a significant change in foraging rates.



Figure 4. (a) Expected foraging rate of small woodland birds based on the best model, with 95% confidence intervals. Foraging rate is number of foraging events per 2ha site per hour
(b) Ratio of expected foraging rates in control and treatment sites before and after the cull. The rightmost plot is the relative difference in the after/before ratio for Treatment and Control. Best model included BACI base model + Area + Forest extent at 1000ha + Total stems.



Figure 5. (a) Expected foraging rate of small woodland birds based on the best model excluding *P. striatus*, with 95% confidence intervals. (b) Ratio of expected foraging rates in control and treatment sites before and after the cull. The rightmost plot is the relative difference in the after/before ratio for Treatment and Control. Best model included BACI base model + Area + Forest extent at 1000ha + Total stems.


Figure 6. Treatment effect by species. Each plot shows the log of the ratio of the expected relative change in foraging rates in the post-cull compared to pre-cull phase for treatment compared to control sites, with 95% confidence intervals. The dotted line at 0 represents a log ratio of 0 i.e. no difference between treatment and control sites in the post-cull compared to pre-cull phase. Bold lines show species that saw a significant change in the amount of foraging in treatment compared to control sites in the post-cull period.

3.4 Discussion

We conducted an experimental removal of an overabundant bird, *M. melanocephala*, whose extreme interference competition is listed as a Key Threatening Process due to its impact on declining small woodland birds. We monitored the effects on both the culled species (Beggs et al. 2019b) and target species (small woodland birds). Our purpose was to test the resource availability hypothesis of competition in the case of interference competition by monitoring foraging and harassment rates of target species. Unexpectedly, we found no evidence of a change in harassment rates following the cull in spite of the decline in *M. melanocephala* abundance. Equally unexpectedly, given the consistent harassment rates, we recorded increased foraging rates for some target species. In the remainder of this discussion, we explore the results of our experiment more fully and consider the significance of our findings for competition theory and for management of overabundant or invasive species that exert their effects through

interference competition. We also discuss some of the limitations to our study and how these might be overcome in future studies.

3.4.1 Qu 1. Does removing an aggressive, overabundant bird reduce interference competition for vulnerable species?

The competitively-dominant species, M. melanocephala, was the aggressor in 66% of harassment events in the pre-cull phase. The reduction in M. melanocephala abundance in treatment sites post-cull was 28% greater than in control sites. We therefore expected a post-cull reduction in the amount of harassment suffered by small woodland birds in treatment sites compared to control sites of approximately $66\% \times 28\% = 18.5\%$. Unexpectedly, we found no evidence of a reduction in harassment of small woodland birds. Indeed, the direction of the effect suggested a relative increase in harassment in treatment sites post-cull (Figure 3). Neither was there evidence of a reduction in harassment of all victim species as a result of the cull (Table S9, Appendix). Due to the extreme collective aggression of M. melanocephala at even low densities, it is possible that the modest reduction in abundance achieved as a result of the cull was insufficient to show any detectable effect on harassment rates. We also considered the possibility that other aggressive species compensated for the decline in harassment due to reduced abundance of M. melanocephala. Because of the role of M. melanocephala in structuring species assemblages (Maron et al. 2013), we term this "social release", analogous to hypotheses such as mesopredator release (Crooks et al. 1999) or competitive release (Kunte 2008). Such an effect has been seen in artificial nest predation studies, for example (Robertson et al. 2014). Compensatory processes are common in management actions that involve removal of overabundant or invasive species (Carter et al. 2007, Choquenot 1991, Marlow et al. 2015). This makes monitoring of outcomes for target species even more important, particularly in cases where compensation involves negative consequences for target species due to unexpected interactions with other species (Norbury et al. 2013, Oppel et al. 2014, Smith et al. 2017) or other disturbances (Doherty et al. 2015). However, due to the low detection rates of harassment and foraging of small woodland birds in this study, we are unable to draw firm conclusions about any social release effect or compensatory responses by other aggressive bird species.

3.4.2 Qu 2. Does removing an aggressive, overabundant bird increase foraging rates for vulnerable species?

In spite of the failure of the cull to reduce harassment rates, there was a twofold increase in foraging rates for target species in treatment compared to control sites following the cull (Figure 4). This effect was ten-fold when we excluded from models the species most commonly observed foraging (Figure 5). The increase in foraging was species-specific, most small woodland bird species detected recording no change in foraging rates (Figure 6). Three species benefitted from the cull by a relative increase in foraging in treatment sites compared to control sites by a factor of between 7.4 and 54.6 (Figure 6). In the case of these three species, this may be a confirmation of the resource availability hypothesis as an explanation of the impact of *M. melanocephala* on small birds (Mac Nally et al. 2005, Maron et al. 2013). However, these three species (L. penicillatus, S.brevirostris and R.leucophrys) were among the commonest small woodland birds observed foraging in study sites and appeared better able to coexist with M. melanocephala than other less common species. Indeed, L. penicillatus and R. leucophrys are themselves aggressive species and accounted for 7.5% and 3.6% respectively of total harassment events in this study (Table S4, Appendix). They were also the only small woodland birds observed to harass *M. melanocephala* (Figure 2).

3.4.3 Interspecific interactions, the distribution of species and unexpected outcomes in field experiments

The counterintuitive combination of increased foraging rates and consistent harassment rates is not easy to explain. According to the resource availability hypothesis of interspecific competition, we would expect these variables to change in inverse proportion to each other. Our study appears to confirm that resource availability, and by extension species co-occurrence, is not solely determined by competition. Whilst distribution of species is influenced by interspecific interactions, a range of other factors also influence it. Many studies have used the geographic distribution of species to infer the effect of interspecific interactions on species assemblages (Connor et al. 2013, Mac Nally et al. 2012, Mönkkönen et al. 2017). Clear causality is hard to prove through co-occurrence networks, however, since interspecific interactions are not the only determinant of species distribution; environmental factors are also significant (Houlahan et al. 2007, Mutshinda et al. 2009, Ricklefs 2013). With respect to competition, co-occurrence studies are also limited in their ability to distinguish the individual effects of a range of interspecific

associations such as positive, facilitative and non-trophic interactions (Bertness et al. 1994, Bruno et al. 2003, Cardinale et al. 2002). Field experiments can more clearly indicate causality and the nature of interactions (Connell 1983, Goldberg et al. 1992, Gurevitch et al. 2000, Schoener 1983) but are often practically limited in scale so the two methods are useful complements. In our case study, in spite of a well-designed experimental approach, a clear causal relationship between competition and resource availability proved difficult to show: the effects of the removal of the key competitive species were limited by an inability to reduce abundance to ecologically significant levels. Despite twice removing M. melanocephala completely from treatment patches (a total of 538 birds at a cost of AU\$13069), compensatory immigration occurred almost immediately (Beggs et al. 2019b). Similar compensatory immigration has been reported in other culls of *M. melanocephala* (Davitt et al., 2018, Grey et al., 1998) and other taxa (Grarock et al., 2012, Kierepka et al., 2017, King et al., 2011, Lazenby et al., 2015). Given the extreme effect of even low densities of *M. melanocephala* on species assemblages, the modest reduction in abundance of *M. melanocephala* achieved by our cull may mean little detectable impact on levels of harassment.

The effects of our failure to achieve substantial reductions in *M. melanocephala* abundance were compounded by our small sample size (eight replicates). Site selection in this agricultural landscape was constrained by the need for high detection rates of *M. melanocephala*, similar vegetation characteristics and a landholder willing to host the study. Combined with the low detection rates of small birds in sites, this meant that the study had low statistical power. Our study is a reminder that the best experimental designs can fail to show what was intended due to unforeseen outcomes.

It is possible that, had we invested in continued culling, we would have achieved more substantial reductions in *M. melanocephala* abundance and therefore seen a greater effect on foraging and harassment rates. The study, however, had a clear aim in assessing the effectiveness of culling as a management tool practically applicable at the enormous scale over which *M. melanocephala* exerts its effects. We considered, therefore, that such expense would be prohibitive in any practical management situation. It may be that in less modified vegetation configurations, culling could be effective (see Crates et al. 2018), but it is essential to know this before committing conservation resources to culling at a broader scale.

A positive outcome of the recolonisation we observed is that it highlights the lack of knowledge of the basic ecology of *M. melanocephala* in the novel ecosystems of this highly modified agricultural region. We do not know from where recolonising

birds came or what drivers encouraged their dispersal. Such information is essential if we are to discover a successful culling configuration. We have retained the bodies of all culled birds from this study for future genetic studies which could indicate relationships between the metapopulations in the two waves of recolonisation. Future banding studies could also aid in determining the origins of recolonising birds and the distances over which they are prepared to disperse to occupy vacated territory.

A further limitation of our study was a possible inherent difference between treatment and control sites. We chose treatment/control replicates with comparable vegetation characteristics and found no inherent differences between treatment and control sites in response of *M. melanocephala* abundance to the cull (Beggs et al. 2019b), in artificial nest predation rates (Beggs et al. 2019a), nor in foraging rates in this study. However, we recorded a large difference in pre-cull harassment rates between treatment and control sites (Figure 3; Figure S5, Appendix). Whether this represents a real difference between treatment and control sites or is simply a random result of the small sample size of harassment events where small woodland birds were victim (N = 41), is difficult to say.

3.4.4 Possible explanations for our counter-intuitive findings

Annual rainfall, the chief determinant of productivity in this region of irregular rainfall, was 59% higher in the post-cull year than in the pre-cull year (Bureau of Meteorology, 2017) (Figure S1, Appendix). Hence, there may have been greater avian activity generally in the post-cull phase due to an increase in resource availability. This might explain the modelled 39% increase in foraging in the post-cull season in treatment and control sites combined (Figure 4, Table S11 - Phase, Appendix). More small woodland birds foraging in sites might then also provide more targets of harassment.

We also considered changes in the proportion of harassment by *M*. *melanocephala* as a possible explanation. While there was no difference in the total amount of harassment conducted by *M. melanocephala* against all victim species in the pre-cull and post-cull phases (Figure S2, Table S9, Appendix), there was a decline in the proportion of total harassment conducted by *M. melanocephala* in treatment sites (Figure S3, Appendix). There is a general belief that harassment by *M. melanocephala* is of greater intensity than harassment by other species because *M. melanocephala* defends territory co-operatively and is perceived to be more persistent in its attacks. Hence, the decline in proportion of harassment by *M.*.

melanocephala could indicate an overall decline in intensity of harassment in treatment sites post-cull. Such a decline in harassment intensity, even without a change in harassment rate, could explain increased foraging. However, when we considered harassment of small woodland birds only (rather than all victim species), there was no change in proportion of harassment by *M. melanocephala* in treatment sites (Figures S4, S5). However, the low detection rates of harassment events of small woodland birds, particularly in treatment sites (Figure 3; Figures S4, S5), mean it is difficult to make firm conclusions about the relationship between foraging rates and harassment rates.

Interestingly, we found that harassment by *M. melanocephala* had neither the biggest mean group size (Figure S6, Appendix), nor the greatest duration (Figure S7, Appendix), nor the greatest intensity (which we defined as the product of harassing group size and duration of attack) (Figure S8, Appendix). GLMMs of harassing group size, duration of attack and harassment intensity showed no treatment effect (Tables S14, S15, S16, Appendix).

3.4.5 Conclusions

Improvements in opportunities for foraging and reproduction are essential if vulnerable species are to recover in the longer term. Hence, for this experiment we monitored changes in foraging opportunities (reported here) and reproductive potential (Beggs et al. 2019a). In addition, we monitored changes in harassment rates to see if interference competition by the dominant aggressor, or other aggressive species associated with high *M. melanocephala* densities, is the reason that small woodland birds are unable to access resources in sites colonised by *M. melanocephala*. We showed that even modest reductions in abundance of the dominant aggressor resulted in greater resource availability for some small woodland birds for up to six months. We were unable to show that this was due to less interference competition so our attempt to link the impact of interference competition to resource availability was not wholly successful.

M. melanocephala has a preference for small, degraded woodland remnants in fragmented landscapes (Maron et al. 2013, Oldland et al. 2009). Such habitat may have a limited capacity to support recovery of target species (Bennett et al. 2015, Cunningham et al. 2014b, Ford 2011, Ikin et al. 2014), even if the threat from *M. melanocephala* is mitigated. Well-designed ecological restoration, particularly where a shrub layer is included, is believed to both deter *M. melanocephala* and support declining small woodland birds (Clarke et al. 2010, Hastings et al. 2006, Lindenmayer et al. 2018, Tulloch et al. 2016b). Managing resource supply through

ecological restoration may therefore be a suitable complementary policy to managing resource demand through culling of interference competitors.

Declarations

Approval for the cull was granted by the New South Wales Office of Environment and Heritage and ethics approval was given by the Australian National University's Animal Ethics and Experimentation Committee (protocol A2016/04). The research was supported by Birdlife Australia, the Holsworth Wildlife Endowment and the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub. The authors are grateful to the landowners for granting access to their land for the study.

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Appendix: additional tables and figures

Tables

Table S1. Types of harassment recorded

Type of harassment	Description
Chase	Aggressor approaches victim aggressively, victim
	leaves, aggressor chases aerially
Supplant	Aggressor approaches victim aggressively and
	takes victim's place
Harassment	Aggressor approaches victim and behaves
	aggressively physically or vocally
Posturing	Aggressor approaches victim with caution, usually at
	a distance and "monitors" the presence of the victim,
	making its presence felt, rather than actively trying
	to evict the victim. This form of aggression was
	mostly recorded for Manorina melanocephala
	behaviour towards larger birds such as Australian
	ravens

Table S2. Landscape- and patch-scale predictors used in models

Predictor	Expected impact on rates of foraging and harassment
Patch-scale features	
Total stems (Average no.	Higher stem densities are likely to have greater resource abundance.
of tree stems in a 20m x	Manorina melanocephala prefers sites with lower stem density (Howes et al.,
20m quadrat at each of	2010). We expected patches with higher stem density to have higher rates of
three marker posts along	foraging and lower rates of harassment.
the 200m site transect in	
each patch)	
Patch area	Smaller patches have relatively more edge, are likely to experience greater
	biotic edge effects (Fischer and Lindenmayer, 2007) and are likely to have
	less habitat diversity than larger patches (Saunders et al., 1991). Among
	biotic edge effects, patches with more edge support higher populations of
	aggresssive generalist species and Manorina melanocephala (Maron et al.,
	2013). We therefore expected more foraging and less harassment in larger
	patches. All our patches were within a narrow range $(4 - 49ha)$ so we did not
	expect a big effect.
Corrected perimeter to	As with patch area above, patches with a higher CPA have relatively more
area ratio (CPA)	edge so are likely to have a greater abundance of Manorina melanocephala
Perimeter	and other aggressive generalist species. Hence, we expected more foraging
$CPA = \frac{1}{\sqrt{Area \times 4\pi}}$	and less harassment in patches with lower CPA.
Hence a circle has a	
CPA of 1 and all other	
shapes have a CPA >1	
Landscape-scale features	
Per cent woodland cover	Greater woodland cover is likely to provide better connectivity for small
at 1000ha	woodland birds (Fischer and Lindenmayer, 2007) and Manorina
	melanocephala density is lower in landscapes with higher tree cover
	(Montague-Drake et al., 2011). We therefore expected more foraging and
	less harassment in patches with higher per cent woodland cover at 1000ha.
Topographic wetness	TWI has been used as a measure of productivity (Montague-Drake et al.,
index (TWI)	2011). Higher productivity may support higher populations of small woodland
	birds but is also associated with higher Manorina melanocephala density
	(Montague-Drake et al., 2011). We therefore made no prediction about the
	influence of TWI on harassment and foraging.

Table S3. No. of harassment events suffered by each victim species (ascending order). An asterisk indicates small woodland birds.

Victim species	No. harassment	% of total
CBr	1	0.4
CP	1	0.4
FTC	1	0.4
HS	1	0.4
M*	1	0.4
NNH	1	0.4
RW*	1	0.4
W*	1	0.4
WNH*	1	0.4
WTE	1	0.4
Mammal (Yellow footed antechinus)	1	0.4
GST*	2	0.8
RWB*	2	0.8
WBW	2	0.8
AH	3	1.2
BFH	3	1.2
Mammal (fox)	3	1.2
NF	3	1.2
PC	3	1.2
SCC	3	1.2
SK	3	1.2
WW*	3	1.2
BTC*	4	1.6
R	4	1.6
RRP	5	2
G	6	2.4
GBB	6	2.4
PBB	6	2.4
St	6	2.4
CSp	7	2.8
LK	7	2.8
SuP	7	2.8
WPH*	10	4
WWC	10	4
NK	11	4.3
BF	12	4.7
AR	13	5.1
ER	13	5.1
AM	15	5.9

NM	16	6.3
BFCS	18	7.1
ML	18	7.1
StP*	18	7.1
Sum	253	100

Table S4. No. of harassment events
conducted by each aggressor
species (ascending order). An
asterisk indicates small
woodland birds.

Aggressor	No.	% of
species	harassment	total
	events 1	0.4
BFH	1	0.4
	1	0.4
HS (exotic)	1	0.4
NK	1	0.4
PC	1	0.4
RF*		0.4
RW*	1	0.4
SK	1	0.4
St (exotic)	1	0.4
GBB	2	0.8
LK	2	0.8
WWC	2	0.8
AR	3	1.2
BFCS	3	1.2
SCC	3	1.2
AH	4	1.6
DB	4	1.6
G	5	2.0
ML	8	3.2
WW*	9	3.6
PBB	10	4.0
AM	18	7.1
WPH*	19	7.5
NM	152	60.1
Sum	253	100

Table S5. Glossary of species names (alphabetical by abbreviated

name). An asterisk indicates small woodland birds.

Abbreviation	Common name	Scientific name
AH	Australian hobby	Falco longipennis
AM	Australian magpie	Cracticus tibicen
AR	Australian raven	Corvus coronoides
BF	Brown falcon	Falco berigora
BFCS	Black-faced	Coracina novaehollandiae
	cuckoo shrike	
BFH	Blue-faced	Entomyzon cyanotis
	honeyeater	
BTC*	Brown treecreeper	Climacteris picumnus
CBr	Common	Phaps chalcoptera
05	bronzewing	
CP	Crested pigeon	Ocypnaps lopnotes
CK		Eudynamys scolopaceus
CSp	Collared	Accipter cirrnocephalus
П	Dollarbird	Fundation orientalia
	Eastern recelle	Eurystomus onemans
	Eastern rosella	Cocomontio flobolliformio
GRR	Galall Grov butchorbird	
GDD CST*	Grey shrike thrush	Collurisingle bermonice
<u>Ц</u> С	House sparrow	Passar domosticus
115	(exotic)	rasser domesticus
IK		Dacelo novaequineae
LIX	kookaburra	Daccionoracganicae
M*	Mistletoebird	Dichaeum hirundinaceum
ML	Magpie lark	Grallina cyanoleuca
NF	Noisy friarbird	Philemon corniculatus
NK	Nankeen kestrel	Falco cenchroides
NM	Noisy miner	Manorina melanocephala
NNH	Nankeen night	Nycticorax caledonicus
	heron	
PBB	Pied butcherbird	Cracticus nigrogularis
PC	Pied currawong	Strepera graculina
R	unidentified raptor	NA
RBE	Rainbow bee- eater	Merops ornatus
RCR*	Red-capped robin	Petroica goodenovii
RF*	Restless flycatcher	Myiagra inquieta
RRP	Red-rumped	Psephotus haematonotus
RW*	Rufous whistler	Pachycephala rufiventris
RWB	Red wattlebird	Anthochaera carunculata
SCC	Sulphur-crested	Cacatua galerita
	cockatoo	J
SFW*	Superb fairy wren	Malurus cyaneus
SK	Sacred kingfisher	Todiramphus sanctus
St	Starling (exotic)	Sturnus vulgaris

StP*	Striated pardalote	Pardalotus striatus
StrTh*	Striated thornbill	Acanthiza lineata
SuP	Superb parrot	Polytelis swainsonii
W*	Weebill	Smicrornis brevirostris
WG*	Western gerygone	Gerygone fusca
WBW*	White-browed woodswallow	Artamus superciliosus
WNH*	White-naped honeyeater	Melithreptus lunatus
WPH*	White-plumed honeyeater	Lichenostomus penicillatus
WTE	Wedge-tailed eagle	Aquila audax
WTG*	White-throated gerygone	Gerygone olivacea
WW*	Willie wagtail	Rhipidura leucophrys
WWC	White-winged chough	Corcorax melanorhamphos
WWT*	White-winged triller	Lalage tricolor
YRTh*	Yellow-rumped thornbill	Acanthiza chrysorrhoa
YTh* Mammals	Yellow thornbill	Acanthiza nana
VF	Vellow-footed	Antechinus flavines
Antech	antechinus	
Fox	European fox (exotic)	Vulpes vulpes

Harassment models

Table S6. Effect size and 95% confidence intervals for modelled effect of cull on harassment rates. Coefficient estimates represent the log of the relative change in expected harassment rate for a change from the reference level of the corresponding BACI variable (N=256 surveys in 16 sites).

	woodland bird species		bird species			
Fixed effects	Coefficient estimate	Lower confidence	Upper confidence	Coefficient estimate	Lower confidence	Upper confidence
-		interval	interval		interval	interval
Intercept	-1.52	-2.42	-0.62	-0.01	-0.48	0.45
Treatment	-1.62	-3.11	-0.13	-0.65	-1.34	0.05
Phase	-0.98	-1.75	-0.21	0.10	-0.21	0.41
Treatment:						
Phase	0.98	-0.60	2.56	0.25	-0.27	0.77
Random effects (log scale)	Variance					
Farm	NA			4.84 x ′	10 ⁻⁸	
Site	0.94			3.23 x ²	10-1	

Best harassment model, victims = small Best harassment model, victims = all

Table S7. Summary of candidate models to explain variation in harassment rates of small woodland birds, constrained by inclusion of BACI base model (Treatment, Phase, Treatment:Phase)

Model	No. of variables	AIC	ΔΑΙϹ
Base + Area + Total stems + TWI	6	213.52	0.69
Base + CPA	4	213.63	0.79
Base + Area + TWI	5	214.19	1.36
Base + TWI	4	214.31	1.48
Base + CPA + FE-1000ha	6	214.66	1.83
Base + CPA +TWI	5	214.76	1.93
Base + Area + CPA	5	214.76	1.93
Base + FE-1000ha	4	214.77	1.94
Base + TWI + Total stems	5	214.77	1.94
Base	3	214.78	1.95
Base + FE-1000ha + Total stems	5	214.81	1.97

Table S8. Summary of candidate models to explain variation in
harassment rates for all victim species, constrained by
inclusion of BACI base model (Treatment, Phase,
Treatment:Phase)

Model	No. of variables	AIC	ΔΑΙϹ
Base + CPA + TWI	5	731.9	0.0
Base + TWI	4	732.0	0.1
Base + CPA + TWI + Area	6	732.8	0.9
Base	3	733.4	1.5
Base + CPA + TWI + Area	7	733.5	1.6
+Total stems			
Base + CPA + TWI + Total	6	733.7	1.8

Table S9. Effect size and 95% confidence intervals for modelled effect of cull on amount of harassment conducted by *Manorina melanocephala* on all victim species. Coefficient estimates represent the log of the relative change in expected amount of harassment by *Manorina melanocephala* for a change from the reference level of the corresponding explanatory variable.

Fixed effects	Coefficient estimate	Lower confidence interval	Upper confidence interval
Intercept	-0.44	-1.05	0.18
Treatment	-0.12	-0.98	0.74
Phase	-0.04	-0.59	0.52
Treatment: Phase	-0.22	-1.09	0.65
Random effects	Variance		
Farm	0.09		
Site	0.34		

Foraging models

Table S10. Summary of candidate models to explain variation in foraging rates of small woodland birds, constrained by inclusion of BACI base model (Treatment, Phase, Treatment:Phase)

Model	No. of variables	AIC	ΔΑΙϹ
Base model + Area + FE-	6	1096.84	0.00
1000ha + Total stems			
Base model + Area + Total	6	1098.30	1.46
stems + TWI			
Base model + Area + CPA	7	1098.54	1.70
+ FE-1000ha + Total stems			
Base model + Area + FE-	7	1098.83	1.99
1000ha + Total stems +			
TWI			

Table S11. Effect size and 95% confidence intervals for modelled effect of cull on foraging rate of small woodland birds. Coefficient estimates represent the log of the relative change in expected foraging rate for a change from the reference level of the corresponding BACI variable. For landscape and vegetation variables, the estimates represent the change in expected foraging rate for a unit change in the variable. (N=256 surveys in 16 sites).

Best forage model i, (Base model + Area + Forest extent at 1000ha + Total stems) Best forage model ii (Base model + Area + Total stems + TWI)

Fixed effects	Coefficient estimate	Lower confidence interval	Upper confidence interval	Coefficient estimate	Lower confidence interval	Upper confidence interval
Intercept	0.87	-0.06	1.81	1.59	0.46	0.69
Treatment	0.64	-0.32	1.61	0.50	0.50	-0.49
Phase	0.33	0.10	0.56	0.33	0.12	0.10
Area	-0.96	-1.57	-0.33	-1.12	0.36	-1.82
FE 1000ha	0.07	0.01	0.14	NA	NA	NA
Total stems	-0.19	-0.31	-0.07	-0.19	0.06	-0.32
TWI	NA	NA	NA	-0.34	0.20	-0.74
Treatment:	0.66	0.34	0.98	0.66	0.16	0.34
Phase						
Random	Variance					
effects						
Farm	2.66 x 10 ⁻	3		1.26 x 10 ⁻⁸		
Site	6.80 x 10 ⁻	1		7.845 x 10 ⁻¹		

Model	No. of variables	AIC	ΔΑΙϹ
Base model + Area + FE-	6	618.12	0.00
1000ha + Total stems			
Base model + Area + CPA	7	618.81	0.69
+ Total stems + TWI			
Base model + Area + Total	6	619.19	1.08
stems + TWI			
Base model + Area + CPA	7	619.35	1.23
+ FE-1000ha + Total stems			
Base model + Area + CPA	8	619.35	1.23
+ FE-1000ha + Total stems			
+ TWI			
Base model + Area + FE-	7	619.53	1.41
1000ha + Total stems +			
TWI			

Table S12. Summary of candidate models to explain variation in foraging rates of small woodland birds (excluding striated pardalote), constrained by inclusion of BACI base model (Treatment, Phase, Treatment:Phase)

Table S13. Effect size and 95% confidence intervals for modelled effect of cull on foraging rate of small woodland birds, excluding commonest species (striated pardalote). Coefficient estimates represent the log of the relative change in expected foraging rate for a change from the reference level of the corresponding BACI variable. For landscape and vegetation variables, the estimates represent the change in expected foraging rate for a unit change in the variable. (N=256 surveys in 16 sites). Best forage model i (Base model + Area Best forage model ii (Base model +

_	+ FE-1000ha + Total stems)		Area + Total stems + TWI)			
Fixed	Coefficient	Lower	Upper	Coefficient	Lower	Upper
effects	estimate	confidence	confidence	estimate	confidence	confidence
		interval	interval		interval	interval
Intercept	-1.23	-3.29	0.82	0.84	-1.42	3.11
Treatment	-0.57	-2.29	1.15	-1.03	-2.98	0.91
Phase	-1.08	-3.12	0.96	0.14	-0.37	0.66
Area	-1.58	-3.13	-0.02	-2.58	-4.71	-0.46
FE 1000ha	0.19	0.05	0.34	NA	NA	NA
Total stems	-0.33	-0.66	0.00	-0.38	-0.77	0.01
TWI	NA	NA	NA	-1.08	-2.07	-0.09
Treatment:	2.34	1.47	3.22	2.35	1.48	3.22
Phase						
Random	Variance					
effects						
Farm	1.36			1.101		
Site	1.20			2.098		

Models of intensity of harassment

Table S14. Effect size and 95% confidence intervals for modelled effect of cull on duration of harassment conducted by *Manorina melanocephala* on all victim species. Coefficient estimates represent the log of the relative change in expected duration of harassment *Manorina melanocephala* for a change from the reference level of the corresponding explanatory variable.

Fixed effects	Coefficient estimate	Lower confidence interval	Upper confidence interval
Intercept	1.72	1.3476	2.0924
Treatment	0.04	-0.352	0.432
Phase	-0.27	-0.6228	0.0828
Treatment: Phase	0.51	-0.0584	1.0784
Random effects	Variance		
Farm	0.15		
Site	7.91 x 10 ⁻⁹		

Table S15. Effect size and 95% confidence intervals for modelled effect of cull on group size of harassment conducted by *Manorina melanocephala* on all victim species. Coefficient estimates represent the log of the relative change in expected group size of harassment by *Manorina melanocephala* for a change from the reference level of the corresponding explanatory variable. Model output shown used a negative binomial distribution. Using a Poisson distribution did not change model AIC.

Fixed effects	Coefficient estimate	Lower confidence interval	Upper confidence interval
Intercept	-0.19	-0.48	0.10
Treatment	-0.30	-0.75	0.15
Phase	0.31	0.04	0.58
Treatment: Phase	-0.10	-0.57	0.37
Random effects	Variance		
Farm	2.91 x 10 ⁻⁹		
Site	8.06 x 10 ⁻²		

Table S16. Effect size and 95% confidence intervals for modelled effect of cullonintensityofharassmentconductedbyManorinamelanocephalaonallvictimspecies.Coefficientestimatesrepresent the log of the relative change in expected intensity ofharassmentbyManorinamelanocephalaforachangefromthereferencelevelofthecorrespondingexplanatoryvariable.

Fixed effects	Coefficient estimate	Lower confidence interval	Upper confidence interval	
Intercept	2.08	1.53	2.63	
Treatment	0.32	-0.28	0.94	
Phase	-0.54	-0.52	0.42	
Treatment: Phase	-0.08	-0.88	0.72	
Random effects	Variance			
Farm	0.32			
Site	0.04			

Figures



Figure S1. Regional rainfall during the period of the study (average monthly rainfall at Bureau of Metereology weather stations Mt Horeb and Old Junee, situated at the eastern and western ends of the study region respectively). The pre-cull monitoring period was October - December 2015; post-cull monitoring was done October - December 2016. The cull of Manorina melanocephala was completed May-June 2016.



Figure S2. No. of harassment events conducted by *Manorina melanocephala* by treatment and phase (all victim species)



Figure S3. Proportion of total harassment events conducted by *Manorina melanocephala* by treatment and phase (all victim species)



Figure S4. No. of harassment events conducted by Manorina melanocephala on small woodland birds by treatment and phase



Figure S5. Harassment events of small woodland birds by aggressor species



Figure S6. Mean group size of aggressors by species

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Figure S7. Mean duration of harassment events by aggressor species



Figure S8. Mean harassment intensity by aggressor species

Chapter 4: An experimental test of a compensatory nest predation model following lethal control of an overabundant native species

Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with <u>https://policies.anu.edu.au/ppl/document/ANUP_003405</u>

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multiauthor papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

Title: An experimental test of a compensatory nest predation model following lethal control of an overabundant native species

Authors: Richard Beggs, Jennifer Pierson, Ayesha I.T. Tulloch, Wade Blanchard, Martin Westgate, David Lindenmayer

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Foreword

Chapter four considers the effect of the noisy miner cull on artificial nest predation rates. Successful reproduction by declining small woodland birds is essential if their populations are to stabilize and recover. Nest predation is the principal cause of breeding failure in temperate eucalypt woodlands of the southeast of Australia and birds are the principal nest predators. Noisy miners are known nest predators and nesting disruptors but a number of other nest predators exist alongside noisy miners. If culling noisy miners is to be applied as a means of improving reproduction by small woodland birds, it is important to know that compensatory nest predation by other nest predators does not occur. Few nesting attempts by small woodland birds are made in woodland colonized by noisy miners due to aggressive nesting disruption by noisy miners. Artificial nest predation studies are therefore the only way to compare nest predation rates before and after removal of noisy miners.

Abstract

Culling of overabundant and invasive species to manage their ecological impacts on target species is widely practised but outcomes are unpredictable and monitoring of effectiveness often poor. Culling must improve ecosystem function, so clear, measurable goals, such as improved breeding potential of target species, are necessary. Many overabundant and invasive species are also nest predators and nest predation is the principal cause of breeding failure of many birds of conservation concern. It is important for managers to know the likely effects on nest predation when culling one species among a suite of nest predatory species. We tested the effect of culling a hyperaggressive, overabundant bird and known nesting disruptor, the noisy miner (Manorina melanocephala), on artificial nest predation rates in remnant eucalypt woodlands in a highly fragmented agricultural landscape of eastern Australia. Culling of noisy miners is already practised to manage this key threatening process, but evidence of improved breeding outcomes for target species is lacking. We found no significant change in artificial nest predation rates following the treatment, despite a 28% reduction in noisy miner abundance in treatment compared to control sites. We identified five other nest predatory bird species, the noisy miner being responsible for 18.3% of total predation. Our findings suggest a compensatory nest predation model, which is problematic for management. It means that, where culling is done with a view to improving breeding potential of target species by reducing nest predation, removing one nest predatory species may not result in a commensurate reduction in nest predation.

Keywords

Overabundant species; invasive species; nest predation; artificial nest predation; cull; compensatory nest predation; additive nest predation
Graphical Abstract



4.1 Introduction

Reducing the population of overabundant or invasive species whose negative ecological impact is a function of their abundance (Carter et al., 2007, Foster et al., 2014) is an intuitively attractive option for wildlife management. Culling has been used as a means of population control for several purposes (Table 1). These include to maintain habitat quality where native herbivores are overabundant (Nugent et al., 2011) and to conserve endangered species by reducing brood parasitism (Rothstein and Peer, 2005), hybridization (O'Loughlin et al., 2017), aggressive competition (Clarke and Schedvin, 1999, Davitt et al., 2018) or predation (Dexter and Murray, 2009, Livezey, 2010, Lazenby et al., 2015).

Many culls have been undertaken without proper monitoring, costing or clear formulation of measurable outputs and outcomes (Rothstein and Peer, 2005, Treves and Naughton-Treves, 2005, Livezey, 2010, Nugent et al., 2011). This is problematic because the outcomes of lethal interventions are unpredictable, compensatory processes are common (Rothstein and Peer, 2005, O'Loughlin et al., 2017) and unexpected or perverse outcomes can occur (Ruscoe et al., 2011, Dexter et al., 2013, Lazenby et al., 2015). Under such uncertainty, a variety of outcomes is possible for the different ecological entities involved (Table 1).

Monitoring programs that measure relevant outcomes of management interventions are of vital importance to reduce uncertainty (Legge et al., 2018, Lindenmayer and Likens, 2018). For management to be effective in the long term, the fundamental objective needs to be improved ecological outcomes for populations of target species.¹ This may include improved access to key resources such as food, and population growth rather than simple population redistribution. Despite this, many studies of the effects of managing invasive or overabundant species consider only the means objective as measured by detection rates of the overabundant or invasive animal (Treves and Naughton-Treves, 2005, Doherty et al., 2015). Some studies also monitor outcomes in relation to the fundamental objective, but this is often limited to detection rates of target species (Grey et al., 1998, Whitfield, 2000, Norbury et al., 2013). Rarely are population processes of target species monitored, such as vital rates.

Breeding success is the main driver of population growth of small birds (Chalfoun et al., 2002, Johnson, 2007) but breeding success is declining in many

¹ In this paper we use the term "target species" to refer to species that management efforts aim to support rather than control.

Table 1. Possible outcomes from management interventions for invasive or overabundant species (bold type indicates overabundant native species, normal

type indicates invasive exotic species).

Fundamental objective achieved (ecological benefit for target species)	Means objective achieved (decline of over- abundant or invasive species)	Ecological process	Ecological response	Published examples
Yes	Yes	Decreased interference competition	Increased abundance and diversity of woodland birds in short term following reduction in abundance of an aggressive, overabundant native bird.	(Grey et al., 1997, Grey et al., 1998)
No	Yes	Other threatening processes (e.g., nest predation, habitat modification); mesopredator release	Abundance of an overabundant brood parasite reduced but no long term increase in population of endangered native birds.	(Rothstein and Peer, 2005)
			No increase in native lizard abundance following removal of exotic predator due to competition from release of exotic rodents.	(Norbury et al., 2013)
			Habitat-specific responses of mesopredators to control of exotic apex predator (feral cat); in some environments, mesopredators (<i>Rattus</i> <i>rattus & R norvegicus</i>) increased nest predation of target species (ground nesting bird).	(Oppel et al., 2014)
			Increased predation on an endangered small native mammal by an exotic mesopredator when a larger exotic predator removed.	(Marlow et al., 2015)
No	No	Compensatory responses: increased reproduction, juvenile survival, immigration	Abundance of overabundant brood parasite returns to pre- management levels within twelve months due to increased reproduction and immigration.	(Rothstein and Peer, 2005)
			Removal of mammalian vector of stock disease ineffective due to immigration; social disruption increases interspecific infection.	(Carter et al., 2007)
			Abundance of overabundant aggressive bird recovers within days due to compensatory immigration.	(Beggs et al., 2019, Davitt et al., 2018)
Not reported	Yes		Reduction in abundance of exotic mesopredators on island.	(Algar et al., 2002)
			Eradication of exotic rodents from islands.	(Howald et al., 2007)

		Population reduction through culling	Reduction in abundance of exotic large herbivores through intensive and persistent culling	(McGregor et al., 2013)
Not reported	No	Compensatory responses: increased reproduction, juvenile survival, immigration	Abundance of overabundant large native herbivore stable in spite of removal, due to immigration	(Osborn and Parker, 2003)
			Culls of invasive mesopredator in forest fragments fail to control population due to immediate recolonization	(King et al., 2011)
			Exotic invasive bird responds to intensive trapping with increased reproduction and immigration	(Grarock et al., 2012)
			Abundance of mesopredator unaffected by intensive trapping, due to compensatory reproduction and immigration	(Kierepka et al., 2017)
Unexpected or perverse outcome	nexpected or Unexpected erverse outcome increase in		Increased abundance of an exotic herbivore when native apex predator removed	(Corbett, 1995)
for target species or other taxa	abundance of overabundant or invasive species	or compensatory immigration; predator release; mesopredator release	Abundance of an apex predator increases in short term following culling	(McKinney, 2001)
			Native & invasive vertebrates more abundant when native apex predator present than when absent	(Newsome et al., 2001)
			Exotic herbivores degrade island vegetation when exotic mesopredator removed	(Bergstrom et al., 2009)
			Endangered native rodent more abundant where a native apex predator occurred, less abundant where an exotic mesopredator occurred due to physical exclusion of the native apex predator	(Letnic et al., 2009)
			Island population of an exotic small predator increases after localized culling	(Bodey et al., 2011)
			Overabundant native herbivores limit recruitment of native vegetation following removal of exotic predator	(Dexter et al., 2013)
			More predation on cattle by younger apex predators when dominant males removed	(MacFarlane, 2014)
			Abundance of invasive mesopredator increases following culling	(Lazenby et al., 2015)

landscapes worldwide (Haskell, 1995, Hoover et al., 1995, Cox et al., 2012b, Okada et al., 2017). In agricultural landscapes, ecosystems are subject to multiple threatening processes that can change species assemblages (Johnson et al 2011). Small woodland birds are in particular decline (Ford, 2011) (but see Ikin et al. (2018)). Along with habitat loss and degradation of key resources for feeding and nesting, some native aggressive species, nest predators and brood parasites have become overabundant (Brittingham and Temple, 1983, Garrott et al., 1993, Rodewald and Arcese, 2016), all of which can have negative impacts on small birds (Andren, 1992, Bayne and Hobson, 1997, Ford, 2011, Mac Nally et al., 2012). Nest predation is the principal cause of breeding failure, particularly among species that construct open cup nests (Martin, 1992, Zanette and Jenkins, 2000, Remeš et al., 2012). Climate change may further increase nest predation rates through synergistic interactions between predators, prey and other environmental stressors such as habitat change (Lumpkin et al., 2012, Ibáñez-Álamo et al., 2015).

One species associated with breeding failure of vulnerable species is the noisy miner (Manorina melanocephala), a co-operatively aggressive, colonial honeyeater. Since European settlement, the noisy miner has become overabundant at a subcontinental scale in the highly modified agricultural landscapes of eastern Australia (Dow, 1977). The species is unique globally in its capacity to structure avian species assemblages, even at densities as low as 0.6 - 0.8 individuals/ha (Mac Nally et al., 2012, Thomson et al., 2015). Small woodland insectivores and nectarivores are declining particularly rapidly in eastern Australia due to both habitat loss and aggressive exclusion by noisy miners (Ford et al., 2001, Paton and O'Connor, 2009, Maron et al., 2013) (but see Lindenmayer et al., (2018b)). Noisy miners impact breeding success of small birds principally through aggressive disruption of nesting activity (Low, 2014) but they have also been observed predating active nests (Crates et al., 2018). Greater abundance of noisy miners is associated with both reduced breeding success of species smaller (<63g) than the noisy miner and increased breeding success in larger species, including known nest predators (Bennett et al., 2015). "Aggressive exclusion of birds from potential woodland and forest habitat by over-abundant noisy miners" was declared a Key Threatening Process under Australian conservation legislation in 2014 (Department of the Environment, 2014).

Some ecologists advocate culling of noisy miners to make woodland fragments available to small woodland birds in time to prevent further declines (Department of the Environment, 2014, Thomson et al., 2015, Mortelliti et al., 2016). Previous experimental removals (Grey et al., 1997, Grey et al., 1998, Debus, 2008, Davitt et al., 2018) have examined only patterns of patch occupancy without considering whether habitat can functionally support important population processes such as breeding. There is currently no published empirical evidence that culling noisy miners will lead to increased breeding success of target species.

In this paper we report on the impact of the noisy miner, and of efforts to manage its abundance through patch-scale culling, on artificial nest predation rates. Small Australian woodland birds suffer some of the highest rates of nest predation in the world (Low, 2014) and in many fragmented landscapes, other bird species are the principal nest predators (Zanette and Jenkins, 2000). For some species of small woodland birds, local evidence suggests that the current breeding rate is insufficient to compensate for adult mortality (Zanette, 2000, Debus, 2006, Gardner and Heinsohn, 2007). Culling of potential nest predators is an attractive management tool to reduce their impacts, but numerous avian nest predators (Guppy et al., 2014) coexist with noisy miners in the "big bird" assemblages that now dominate woodland fragments in eastern Australia (Maron et al., 2013). Few data exist on the relative roles of these different nest predators in limiting breeding success of small woodland birds (Fulton, 2018), nor on the possible role of noisy miners, as strongly interacting species (Montague-Drake et al., 2011, Maron et al., 2013), in controlling levels of nest predation by other nest predators. Many studies have indicated the rise in other nest predatory species in fragmented landscapes or their role in nest predation (Ford, 2011, Bennett et al., 2015, Okada et al., 2017, Crates et al., 2018). In the fragmented landscapes favored by noisy miners, the risk therefore exists that removing noisy miners to increase breeding success of small woodland birds could simply allow greater nest predation by larger generalist species, such as Australian magpie (Cracticus tibicen), pied butcherbird (Cracticus nigrogularis) and pied currawong (Strepera graculina), moving into fragment edges from the agricultural matrix.

Two models exist to explain the effect on nest predation rates of reducing abundance of nest predators. Additive nest predation means that a change in density of a given predator will change predation rates in proportion to that change in density (Tewksbury et al., 2006, Robertson et al., 2014, Smith et al., 2016). Where compensatory nest predation operates (Oppel et al., 2014), a change in density of a given nest predator will not affect the overall rate of predation as other nest predators will compensate for the foregone predation. Knowing which nest predatory mechanism is operating can help us predict whether controlling one nest predatory species is likely to result in improved breeding success for target species (Oppel et al., 2014). In a correlative study of noisy miner density and artificial nest predation rates, Robertson et al. (2014) suggested that the presence of noisy miner colonies invalidated the additive predation model. This they attributed to the keystone role of

noisy miners in structuring species assemblages, suggesting that even in sites with greater density of nest predators, the presence of noisy miners limits the rate of nest predation. However, meaningful application of additive or compensatory nest predation models to assemblages associated with noisy miner colonies is founded on a nest predatory role for noisy miners. Noisy miners predate artificial nests (Major et al. 1996; Crates R, 2018, personal communication), but for real nests, noisy miners are generally associated with nesting disruption through aggressive harassment of small birds or nest destruction (Low, 2014) rather than direct nest predation. Whilst the mechanisms in these two situations are different, nest predation being a form of resource use, nesting disruption being a form of interference competition, the immediate outcome, nest failure, is the same. Recent evidence of noisy miners predating active nests of a small (39g - 45g) (Higgins et al., 2001) honeyeater (Crates et al., 2018) seems to confirm that the two mechanisms are not distinct ecologically.

The implication of the observation by Robertson et al. (2014) that the presence of noisy miners invalidates the additive nest predation model is that a compensatory model is acting. Hence, we may surmise that if noisy miner abundance is reduced through culling, then other nest predators will compensate for the foregone predation. If this is the case, we propose that a better descriptor for the mechanism may be "social release." This is analogous with other forms of ecological release, such as mesopredator release (Soulé et al., 1988) or release from interspecific competition (Bolnick et al., 2010), where removal of an environmental limiting factor allows access to previously unavailable resources. A "social release" mechanism would attribute any effect of removing noisy miners on nest predation rates to responses of other nest predatory species to changed interspecific social relations within the assemblage. Whilst this is a compensatory response, it is not compensatory in the original sense of opposition to additive predation. Crucially, a "social release" model is not contingent on making a distinction between the role of noisy miners as nest predators and nest disruptors.

We present empirical evidence of the effects on artificial nest predation rates of culling noisy miners. We completed a controlled and replicated experimental cull of noisy miners in remnant woodland patches (Beggs et al., 2019). We conducted artificial nest predation experiments before and after the culling treatment and used camera traps to identify nest predators. We used artificial nest predation rate as a proxy for potential breeding success of vulnerable small woodland birds. Artificial nest predation experiments cannot replicate the complex predator-prey relationships that exist around real nests (Major and Kendal, 1996, Zanette, 2002, Thompson and Burhans, 2004). They are, however, used widely as a means of identifying potential

predators, comparing nest predation rates under different ecological conditions, and quantifying susceptibility of different nest types to predation (Zanette, 2002, Vetter et al., 2013, Selva et al., 2014, Fulton, 2018). Given that few breeding attempts are made by small woodland birds in areas dominated by noisy miners (Low, 2014), artificial nest studies provide the only means of comparing nest predation rates between sites with different densities of nest predators (Robertson et al., 2014). They are also the only method to determine if a cull of noisy miners is likely to reduce overall nest predation. Combined with camera monitoring, artificial nest predation experiments can therefore provide essential information about breeding potential of small birds in landscapes dominated by aggressive nest–predatory species.

We aimed to answer two questions:

Qu 1. Does a cull of noisy miners change the rate of artificial nest predation?

Qu.2. What is the contribution of noisy miners to total artificial nest predation?

Based on our "social release" interpretation of a compensatory nest predation model, our *a priori* expectation was that the noisy miner cull would not impact artificial nest predation rates. We expected other avian species of nest predators to compensate for any decline in predation by noisy miners. However, in spite of twice removing all noisy miners from treatment patches, noisy miner abundance in treatment sites post-cull was only 28% lower than in control sites, due to recolonization (Beggs et al, 2019). We were unsure if this was a sufficient reduction to show any compensatory effect.

The highly complex co-operative social organization of noisy miners (Dow, 1970, Dow, 1979) creates an additional uncertainty. Given the social disruption implicit in a cull and recolonisation, we expected a change in the interspecific aggressive behavior of recolonizing noisy miners. Social disruption through culling has been shown to change interspecific competitive interactions in several taxa and in some cases to result in perverse management outcomes (Carter et al., 2007, King et al., 2011). In a recent published study of a noisy miner cull, disruption of intraspecific social relations between recolonizing noisy miners was suggested as a possible explanation for an initial rise in detection rates of small woodland birds following the cull (Davitt et al., 2018). We considered that a similar effect could occur in our study, allowing greater nest predation by other nest predators post cull. The outcome would be in the same direction as any "social release" effect of reduced noisy miner density. Due to the lack of data on the relative contribution made by different nest predatory species to overall predation rates (Fulton, 2018), we made no predictions about the contribution of noisy miners to total artificial nest predation.

4.2 Methods

4.2.1 Study area

This study was conducted from 2015 to 2017 in the South West Slopes region of New South Wales in south-eastern Australia. The region has a continental temperate climate characterised by hot summers and cold winters. Average annual rainfall is 700mm (Bureau of Meteorology, 2016). Historically, the habitat was productive grassy box gum open woodland, which is now a Threatened Ecological Community with more than 85% of its original extent cleared for cropping and grazing and the majority of remnants on private land (Office of Environment and Heritage 2015). A photograph of a representative study site is given in Figure S1.

The study was located within the South West Slopes Restoration Study, a long term ecological monitoring program of woodland remnants conducted by the Australian National University. This program has conducted annual monitoring of birds in woodland patches since 2002, which has indicated long-term declines in many small woodland passerines accompanied by increases in range and abundance of the noisy miner and larger aggressive generalist species (Cunningham et al., 2008, Mortelliti and Lindenmayer, 2015).

4.2.2 BACI Study design

We conducted artificial nest predation experiments between October and December in study sites in the pre-cull 2015/16 breeding season and post-cull 2016/17 season according to a BACI (Before-After-Control-Impact) design to account for annual environmental variations in bird occupancy and nest predation rates.

Eight pairs of patches of remnant or regrowth native eucalypt woodland were selected across seven farms in the shires of Gundagai ($35^{\circ}03'55.5''S 148^{\circ}06'18.7''E$) and Junee ($34^{\circ}52'11.7''S$, $147^{\circ}35'07.9''E$) (Figure 1). Each patch in a pair was randomly allocated to treatment or control and a standardised two-hectare study site was randomly located within each patch. As a result, six farms had one replicate pair of sites and one farm had two pairs. Study patches ranged in size from 4 to 49ha (mean = 13ha) and were at least 1142m apart (mean = 2224m, maximum = 6405m) to minimise spatial dependence and to discourage recolonisation of treatment sites from control sites following the cull. This was based on Dow's (1979) indication of a noisy miner home range of about 200m (diameter of maximum polygon). Noisy miners were present in all patches with consistent detection rates in monitoring since 2002 of at least 20% (Mortelliti et al., 2016).



Figure 1. Study region in south-eastern Australia.

 a) Paired treatment/control study patches on seven farms. Numbers in boxes refer to farm number. b), c) Maps showing relationship of treatment and control patches, and landscape configuration, on two representative farms. b) is Farm 2; c) is Farm 4.

Woodland birds are impacted by changes at site and landscape scales (Montague-Drake et al., 2011, Cunningham et al., 2014). To minimise variance at the site scale, paired woodland fragments were chosen for similar vegetation characteristics based on a rapid visual assessment. Each farm was considered to be an ecological unit within which management of woodland patches was the same and within which the surrounding landscape was largely the same (Cunningham et al., 2007). The presence of one or more treatment/control replicates on each farm aimed to minimise variance at farm and landscape scales.

4.2.3 Experimental treatment

We conducted culls using a 12-gauge shotgun and number 9 shot during the non-breeding season in May and June 2016. We completed two culls at each treatment site within four weeks of each other. We considered a cull complete when there was no visual or vocal response to a 45-minute playback of noisy miner calls. Full methodology and costings are given in Beggs et al., (2019).

4.2.4 Artificial nest predation experimental protocols

Two proprietary aviary nest types were used to simulate the nests of the main small woodland bird groups likely to use such sites and to indicate differences in nest predation rates of the two types:

i. wicker dome nests, diameter 12cm, covered in jute matting to simulate nests constructed by finches, weebills and thornbills (Figure S3(a), Supplementary Material)

ii. open cup nests, diameter 7cm, to simulate nests of robins, whistlers, flycatchers and honeyeaters (Figure S3(b), Supplementary Material)

One plasticine egg was placed in each nest (Zanette and Jenkins, 2000, Guppy et al., 2014). These were fashioned by hand and rolled in broken straw to simulate the surface texture and colour of real eggs. To ensure that possible olfactory-directed mammalian predation was not excluded (Whelan et al 1994, Ibáñez-Álamo et al., 2015), nor that the smell of plasticine would favour detection by rodents (Rangen et al., 2000), nests and eggs were sprinkled with dry chicken faeces and sealed in a plastic bag for 3 days prior to deployment.

We conducted three replicates of the artificial nest predation experiments in each phase of the study. In each replicate we deployed three nests of each type at each site. Hence, there were 72 observational units of each nest type per treatment per year (3 nests x 8 sites x 3 replicates). We attached nests to branches at about 1.5m above ground level using wire and made a rapid visual assessment of foliage cover on a scale of 1 (low) to 3 (high). In each site we installed an infrared-activated camera at as many of each nest type as stocks of equipment permitted. Because of the low predation levels of dome nests, after the first replicate of the artificial nest predation experiment we deployed our limited supply of cameras on cup nests only. We positioned nests in different locations for each replicate to minimise the risk of learning by nest predators (Ibáñez-Álamo et al., 2015).

A previous nest predation study in the region indicated that over 70% of nests were predated within five days of deployment (Okada S, 2015, personal

communication). We therefore left nests *in situ* for five days, then removed them and assessed the nests and eggs visually to determine if they had been predated.

4.2.5 Estimating density of avian nest predators

We conducted eight fifteen-minute bird surveys in each site in both the pre- and post-cull breeding seasons. Surveys consisted of a fifteen-minute walking count of all species present up to 50m either side of the 200m transect. We found that this walking method improved detection of noisy miners, which are vociferous and mobile while the observer is moving but often become still and silent when the observer stops. To estimate density of nest predators for the purposes of the nest predation experiments, we used the average density of each nest predatory species identified in sites in the three surveys closest in time to the experiment.

4.2.6 Experimental variables

Our aim was to assess the impact of the culls of noisy miners on the binary response variable, artificial nest predation, accounting for other factors we expected to influence the response. These factors included our BACI variables (phase, treatment, treatment:phase interaction), other experimental variables (nest type, foliage cover and replicate), landscape and patch scale characteristics, and density of known nest predators (Table 2). We tested these variables for multicollinearity and as a result removed woodland extent at 100ha and 10 000ha and removed Topographic Wetness Index (TWI) from models that included noisy miner density.

Proximity to patch edge has been shown to influence artificial nest predation rate (Ibáñez-Álamo et al., 2015). We used corrected perimeter to area ratio (CPA) as a measure of the relative amount of edge in each site. CPA indicates patch shape complexity irrespective of patch area and is calculated as follows (Kluza et al., 2000):

$$CPA = \frac{Perimeter}{\sqrt{Area \times 4\pi}}$$

Hence, a circle has a CPA of 1 and all other shapes will have CPA >1.

Table 2. Explanatory variables used in GLMMs

Predictor	Expected impact on artificial nest predation rate	Variable	Values
		type	
BACI variables	•		
Treatment		Categorical	Treatment, control
Phase		Categorical	0,1
Experimental variables	·		
Foliage cover	Better concealment of nests is likely to reduce predation (Colombelli-Négrel and	Categorical	1,2,3 (1 indicates
	Kleindorfer, 2009)		low foliage cover)
Nest type	Cup nests are predated more than dome nests (Okada et al., 2017)	Categorical	Cup, dome
Replicate	Learning by nest predators (Ibáñez-Álamo et al., 2015). This could be either that there	Categorical	1,2,3
	are nests there for predation, or that the eggs are artificial and therefore not worth		(1 is the first
	predating.		replicate)
Patch-scale features			
Total stems (Average no. of tree	Noisy miners favour sites with lower stem density (Howes et al., 2010). We therefore	Continuous	1 – 15.7
stems in a 20m x 20m quadrat at	expected sites with higher stem density to have lower nest predation rates.		Mean $= 5.1$
each of the three marker posts along			SD = 4.0
the 200m site transect in each patch)			
Patch area	Patch area influences noisy miner density	Continuous	3.3 – 48.5ha
	(Lindenmayer et al., 2018a, Maron et al., 2013)		Mean = 13.0ha SD =
			10.9
		1	1

Corrected perimeter to area ratio	Patches with a higher CPA have relatively more edge so are likely to have more nest	Continuous	112.9 - 397.0	
(CPA)	predation (Ibáñez-Álamo et al., 2015)		Mean = 196.3 SD =	
			85.6	
Landscape-scale features	·			
Per cent woodland cover at 1000ha	Noisy miner density is lower in landscapes with higher tree cover (Montague-Drake et	Continuous	0.04 – 23.5% Mean	
	al., 2011).		= 3.8%	
			SD = 6.7%	
Topographic wetness index (TWI)	TWI has been used as measure of productivity and has been shown to influence noisy	Continuous	-1.2 - 3.0	
	miner density (Montague-Drake et al., 2011). Other than in models which included		Mean $= 1.1$	
	noisy miner density, we included TWI as we considered it might be associated with		SD = 1.2	
	increased nest predation due to noisy miners.			
Density of avian nest predators				
Density of noisy miners	According to the additive predation model, more nest predators will mean more nest	Continuous	0 - 15/2ha	
	predation (Oppel et al., 2014).		Mean = 4.5/2ha	
			SD = 3.1/2ha	
Density of other known nest		Continuous	0 - 12/2ha	
predators			Mean = 3.6/2ha	

4.2.7 Statistical analysis

4.2.7.1 Qu.1. Does a cull of noisy miners change the rate of artificial nest predation?

4.2.7.1.1 Model selection

Using the glmmTMB package in R version 3.3.2 (R Core Team, 2017), we fitted a global generalized linear mixed effects model (GLMM) with binomial distribution and logit link function (Zuur et al., 2013) using all predictor variables (Table 2). To account for differences in response at site and farm level over repeated artificial nest predation experiments, we used Site and Farm as random effects (Zuur et al., 2009). We used standard diagnostics to check that model assumptions were not violated.

We used R package MuMIn (Barton, 2018) to assess all possible models using all combinations of explanatory variables in the global model. Using Akaike Information Criterion (AIC) score to assess parsimony and fit (Burnham and Anderson, 2003), we selected candidate best models from those models which included the base model, as the Treatment:Phase interaction in the base model represented our treatment effect.

4.2.7.1.2 Model interpretation

The Treatment:Phase interaction indicates differences in response between treatment and control sites from the pre-cull to the post-cull phase. The logit model gives the coefficients of explanatory variables on the logit (log odds) scale. We report results back-transformed to give the expected odds of artificial nest predation, given constant values for other explanatory variables (see Supporting Information, "Calculating expected odds of artificial nest predation," for a more complete explanation of this approach). We report 95% confidence intervals. For simplicity of interpretation, we completed an inverse logit transformation to convert odds in model output to probability.

4.2.7.2 Qu 2. What is the contribution of noisy miners to total artificial nest predation?

We calculated the proportion of total nest predation (across all sites and both phases of the experiment) where a predator was identified on camera, by species of nest predator. We aimed to use regression models to assess the impacts of the density of identified nest predators, BACI variables, and patch and landscape configuration, on the proportion of total predation done by noisy miners and other nest predators respectively. Positive identifications of nest predators were too few to allow a multinomial linear regression of predator identity by BACI, landscape and patch variables. We therefore aggregated all predation done by species other than the noisy miner into a single category, "other predators," to allow us to conduct a binomial model. Zero predation by noisy miners was recorded in control sites before the cull, which caused complete separation in this model. We used R package Logistf, to run a Firth logistic regression, with fixed effects only, to reduce the bias due to this zero value (Heinze and Ploner, 2016). This method provides a penalized likelihood and uses a Wald test to calculate confidence intervals. We used a Fisher's Exact Test to determine if there were any significant differences in predator identity due to Treatment, Phase or overall.

Additionally, we ran a GLMM using BACI variables to test whether there was a relationship between the treatment and the density of other predators. This was to see if any compensatory predation effect observed was simply due to a greater density of other nest predators following removal of noisy miners.

4.3 Results

Expected probability of artificial nest predation declined in both treatment and control sites following the cull (Figure 2a). The odds ratio of the change in probability of artificial nest predation in treatment compared to control sites following the cull was 0.73 (0.33, 1.61) (Figure 2b, rightmost plot). The corresponding decline in noisy miner abundance was by a factor of 0.72 (0.54, 0.95) (Figure S6b, rightmost plot). Of 576 nests (half cups, half domes) placed over the two breeding seasons of the study, 207 (36%) were predated. 54% of cup nests were predated compared to 16% of dome nests (Figure 3). Almost half (132) of the 268 nests monitored with cameras were predated. Of these we were able to identify a nest predator in 60 cases. 95% of identified nest predators were birds. We identified five species of avian nest predator besides noisy miners (Figure S3). We recorded four cases of a mammal investigating or predating nests.

4.3.1 Qu.1. Does a cull of noisy miners change the rate of artificial nest predation?

From models constrained by inclusion of the base BACI variables (Treatment, Phase, Treatment:Phase), eight candidate models had AIC scores within two units of each other (Table S5). We chose the most parsimonious of these as our best model. This model contained the base BACI variables plus Foliage cover, Nest type,



Figure 2. (a) Expected probability of artificial nest predation according to the best model, with 95% confidence intervals; (b) Odds ratios of artificial nest predation before and after the cull in treatment and control sites respectively, with 95% confidence intervals. The dotted line at 1.0 represents a ratio of 1 i.e. no difference between the expected odds. The rightmost plot is the relative difference in the odds ratios between Treatment and Control before and after the cull.



Figure 3. BACI predation rates of cup and dome nests, with standard error

CPA, Replicate and Phase:Nest type interaction. According to this model the decline in artificial nest predation rate was greater in treatment than control sites: the cull resulted in odds of artificial nest predation in treatment sites 0.73 (0.33, 1.61) times odds of artificial nest predation in control sites (Figure 2b). Figure S5 shows the relative effects on artificial nest predation rates of the other variables in the best model (CPA, Foliage Cover, Nest type and Replicate).

4.3.2 Qu 2. What is the contribution of noisy miners to total artificial nest predation?

Noisy miners were responsible for 18.3% of total predation events where the predator was identified (Table 3). The Australian magpie (*Cracticus tibicen*) made the single greatest contribution to total nest predation (27%) (Figure S3). No nest predation by noisy miners was captured on camera in control sites before the cull so it is difficult to give a feasible estimate of the likely amount of predation by noisy miners under "normal" circumstances. Proportions of total nest predation in the pre-and post-cull phase by the different nest predators identified on camera are given in Figure S4.

In treatment sites, artificial nest predation by noisy miners, as a proportion of total predation where a predator was identified, increased from 27.8% before the cull to 33.3% after the cull. In control sites, noisy miner predation increased from 0% before to 10% after (Table 3).

Phase	Predator	Control	Treatment
Before cull	Noisy miner	0	5
	Other	11	12
After cull	Noisy miner	2	4
	Other	18	8

Table 3. Nest predator identity by Treatment and Phase

Our binomial model of predator identity (noisy miner/other) using the Firth logistic regression showed very high uncertainty for the Treatment:Phase interaction term. We found no evidence of a significant change in the proportion of nest predation done by particular nest predators as a result of the cull. 95% confidence intervals for the Treatment:Phase interaction term overlapped zero (Table S6). Fisher's Exact Test for significant differences in identity of nest predators returned

a p-value of 1 for Phase, 0.019 for Treatment and 0.076 overall. Our GLMM using BACI variables to assess the effect of the treatment on density of other nest predators found no relationship (p = 0.84).

4.4 Discussion

We set out to empirically test the effects of a widely proposed and locally practiced management action for a key threatening process. We aimed to determine if patch-scale culls of an overabundant bird have the potential to improve breeding outcomes for declining small birds and to investigate whether there is a compensatory effect of the cull on artificial nest predation rates consistent with our "social release" hypothesis. We found no evidence of a greater decline in post-cull nest predation rates in treatment compared to control sites, consistent with a compensatory nest predation model. We found that noisy miners accounted for 18.3% of total artificial nest predation events where a predator was identified. In the remainder of this discussion we consider our research questions further and suggest how our findings might inform management options to improve breeding potential of small woodland birds.

4.4.1 Qu.1. Does a cull of noisy miners change the rate of artificial nest predation?

There was no evidence of a post-cull difference in the change in artificial nest predation rates in treatment compared to control sites (Figure 2b). This suggests some form of compensatory response. The direction of the small change observed was consistent with an additive nest predation model but there was much heterogeneity in our data such that confidence intervals for odds ratios were wide and overlapped a value of one. This may have been due to the low power of our study given the small number of study sites. Due to our limited camera capture of nest predators, we are unable to say whether the response observed was due to compensatory nest predators. We found no evidence of a change in density of other nest predators following the cull. If other nest predators were responsible for the compensatory nest predation post-cull (rather than recolonizing noisy miners), this points to a change in nest predatory behavior by other nest predators rather than a change in their abundance.

4.4.2 Qu.2. What is the contribution of noisy miners to total artificial nest predation?

Noisy miners were responsible for around a fifth of total identified nest predation events. Other large birds common in the "big bird" assemblages associated with noisy miner colonies accounted for almost all the other predation events. This concurs with another study in the region which found that noisy miners accounted for 22% of identified predations of real nests of a medium-sized, cup-nesting honeyeater (Crates et al., 2018).

The proportion of total artificial nest predation attributable to noisy miners was 18.5% (Table 3). The relative reduction in noisy miner abundance in treatment sites was 28% (Figure S6). Hence, the expected reduction in artificial nest predation post cull under a linear additive model would be $18.5\% \times 28\% = 5.2\%$. The actual relative reduction according to the observed mean odds ratio (Figure 3b) was an unexpected five times greater.

Where the combined impact of other nest predators exceeds that of the species singled out for culling, culling is less likely to have benefits for breeding success of target species (Fulton, 2018). However, if the cull of a strongly-interacting species such as the noisy miner creates a disproportionate decline in artificial nest predation, as may be the case in this study, it may be that a cull can result in lower overall nest predation. Given that predation of real nests of small woodland birds in the region can be as high as 70% (Belder et al., 2018), any reduction in predation is likely to be beneficial.

4.4.3 Uncertainty in achieving fundamental and means objectives

Culling overabundant or invasive species is an intuitively attractive management response. Its effects, however, are unpredictable with regard to both density of the threatening species and outcome for the target species (Table 1). Multiple practical and ecological factors can limit the success of culls (Doherty and Ritchie, 2017). Our experimental cull was no exception. Despite substantial culling effort and expense (Beggs et al., 2019), we failed to reduce the density of noisy miners below the published impact threshold of 0.6 - 0.8 individuals/ha (Mac Nally et al., 2012, Thomson et al., 2015) due to recolonization.

4.4.4 Interspecific and intraspecific social disruption and the potential for perverse outcomes

The role of noisy miners in nest predation is complicated by their influence on the structure and behavior of avian assemblages, particularly with respect to social associations between noisy miners and other nest predators (Fulton, 2008, Robertson et al., 2014). In their refutation of the additive nest predation model, Robertson et al. (2014) showed that increasing densities of some nest predators associated with higher densities of noisy miners were not associated with increased levels of artificial nest predation. Hence, the potential exists for higher levels of nest predation following removal of noisy miners due to "social release," whereby noisy miners no longer exert social control over other nest predators. A similar process has been suggested as an explanation for greater detection rates of small woodland birds following a cull, even where noisy miner density remained above ecological impact thresholds (Davitt et al., 2018). Unexpected or perverse outcomes for target species due to social disruption of overabundant or invasive species following culling have been reported in several other investigations (McKinney, 2001, Bodey et al., 2011, MacFarlane, 2014). We saw no evidence of such an effect in this study, nor of a relationship between the culling treatment and density of other nest predators.

4.4.5 Limitations of the study

A fundamental problem in our experiment was the failure of the cull to reduce noisy miner density below published impact thresholds, in spite of twice removing all noisy miners from treatment sites (Beggs et al., 2019). The study was focused on providing practical management recommendations regarding the impact of culls on potential breeding success of target species. We therefore chose not to continue to cull, considering costs to be prohibitive in any real-world management situation. It is possible, therefore, that noisy miners were not controlled sufficiently to allow for a clear response by other species.

Clear indications of the relative roles of different nest predators were impeded by our limited camera capture data. Whilst the 45% success rate of our camera captures appears low, it is higher than that achieved in similar studies of both real and artificial nests (Robertson et al., 2014, Okada et al., 2017, Belder, 2018, unpublished data). Technical challenges associated with camera use are widely reported (Cox et al., 2012a). In our study, oversensitivity of cameras in a hot environment meant that SD cards filled or batteries failed before the full five days of monitoring were complete. At the same time, adjusting to lower sensitivity meant that predators were not always captured. These challenges could mean that we simply failed to build enough conclusive evidence of a compensatory or additive nest predation model with regard to particular species of nest predator.

Our aim was to compare artificial nest predation rates before and after the cull to see if a cull had the potential to improve breeding success of target species through lowering nest predation rates. Importantly, artificial nest predation rates cannot replicate the complexity of real interactions between predator, prey and environment (Major and Kendal, 1996, Zanette, 2002, Thompson and Burhans, 2004). We therefore make no inferences from our study about nest predatory behavior of particular species towards real nests, which would require experiments in landscapes with active nests.

4.4.6 Threatening processes at multiple scales and implications for management

Breeding is an essential population process that must be supported by environmental management if threatened species are to recover. Where overabundant or invasive species are identified as a threat to breeding success, removing them can only have a successful conservation outcome if threats by other species or processes, which may include predation, nest predation or brood parasitism (Rothstein and Peer, 2005, Livezey, 2010), do not compensate for the reduction in abundance of the targeted threat. Other studies in the region indicate that small woodland birds are subject to up to 70% nest predation even in sites where noisy miner abundance is low (Belder et al., 2018). In another study, noisy miners were observed destroying nests of the critically endangered regent honeyeater (Anthochaera phyrgia) but accounted for only two out of 23 identified artificial nest predation events (Crates R, 2018, personal communication). Whilst there is some evidence that controlling noisy miners improved breeding success, even where noisy miner numbers were controlled, and none predated nests, breeding failure due to nest predation remained high (Crates et al., 2018). Similar outcomes have been seen in North America where culling programs for overabundant cowbirds in highly modified agricultural landscapes have failed to improve breeding success of target species due to other threatening processes, including nest predation (Rothstein and Peer, 2005).

The threats to target species represented by overabundant or invasive species operate within the context of a range of threatening processes at multiple scales and predicting outcomes of management of individual processes is rarely straightforward (Dukes et al., 2009, Norbury et al., 2013, Tulloch et al., 2018). At the nest and patch scale, understanding whether additive or compensatory processes operate following

culling is essential in making effective management decisions. In the context of bird assemblages associated with the noisy miner, such questions are hard to answer with artificial nest predation studies because the principal effect of noisy miners on breeding success of smaller woodland birds is not on nest predation but through nesting disruption. We saw no effect of the cull on artificial nest predation rates in this study, suggesting a compensatory response. We therefore recommend further work in this area before culling of noisy miners is recommended more generally. The fixed rate of nest predation inherent in the additive model means that the relationship between management effort to reduce the abundance of the nest predator and the effect on the vital rate of the target species is predictable. The compensatory model presents greater challenges for management since a successful reduction in abundance of one nest predator may not result in any change in vital rate for the target species. This is also the case if the compensatory effect suggested by our "social release" hypothesis is true, such that even after removing noisy miners, other species of nest predator continue to be responsible for high, or even elevated, rates of predation.

At the landscape and patch scale, vegetation condition can influence nest predation rates through both resource availability and its effects on abundance of generalist nest predators (Tewksbury et al., 2006, Robertson et al., 2014, Okada et al., 2017). An understanding of the interaction between vegetation configuration and outcomes of a cull of overabundant or invasive species is essential. The contrasting success of experimental noisy miner culls in the 1990s (Grey et al., 1997, Grey et al., 1998) and more recently (Beggs et al., 2019, Davitt et al., 2018), is an indication that much is still unknown. Native nest predators are not a functionally novel threat to target species in the way that invasive species can be (Smith et al., 2016). Many native species have evolved defensive strategies to nest predation (Ibáñez-Álamo et al., 2015). It is only through the interaction of habitat modification with the existing predatory pressure, that the natural pressure becomes a threatening process. This is very much the case with the noisy miner. Efforts to improve ecosystem function through vegetation restoration, in particular by increasing structural complexity, may ensure a more effective and long term benefit for declining small woodland birds (Grey et al., 2011, Lindenmayer et al., 2018a).

Some idea of the likelihood of achieving fundamental objectives is necessary before seeking to apply expensive means objectives, such as culling programs, more broadly. Empirical studies such as this one, or effective monitoring of existing management programs, are an essential aid to deploying conservation resources more effectively (Lindenmayer and Likens, 2018, Tulloch et al., 2018). Persistence of small woodland birds in agricultural landscapes may be improved by expanding the total available resource base available to them following population reductions of aggressive overabundant native species such as the noisy miner, as noted in previous experimental culls (Grey et al., 1997, Grey et al., 1998). This is likely to be particularly significant in times of resource scarcity such as drought (Mac Nally et al., 2009). However, any management attempt to reverse the decline of vulnerable species in the longer term needs to show improved reproductive outcomes if we are to avoid wasting conservation effort on simply redistributing existing populations across the landscape.

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Supplementary material



Figure S1. Typical study site, showing widely dispersed trees and lack of understory (source: Corresponding author)



Figure S2. Nest types used in study. a) Dome, b) Cup. (Source: Corresponding author)



Figure S3. Contribution of nest predators to total nest predation over the whole study (Treatment and Control sites combined)



Figure S4. Contribution of nest predators to total artificial nest predation in treatment and control sites respectively



Figure S5. Effects of other significant explanatory variables on odds ratios of artificial nest predation.

Odds ratios of nest predation for categorical variables are with respect to reference values Nest type cup, Foliage cover 1 and Replicate 1 respectively. For example, the plot for Nest type dome represents the ratio

Expected odds of artificial nest predation in dome nests Expected odds of artificial nest predation in cup nests

For the continuous variable, CPA, the plot indicates that a one unit increase in CPA corresponds to an expected reduction in odds of nest predation of 0.75.



Figure S6. (a) Expected noisy miner abundances over the two breeding seasons of the study, with 95% confidence intervals.

The dotted line at 1.2 birds/2ha is the impact threshold of noisy miner abundance on species assemblages (Thomson et al 2015). (b) Relative differences in expected noisy miner abundance in the breeding seasons before and after the cull in treatment and control sites respectively, with 95% confidence intervals. The dotted line at 1.0 represents a ratio of 1 i.e. no difference between the expected abundances. Rightmost plot represents the Treatment:Phase interaction effect i.e. the relative difference in the change in noisy miner abundance between treatment and control sites shown in the previous two plots.

Calculating expected odds of artificial nest predation (ANP)

Regression equation for best model (ignoring random effects)

Ln expected odds of ANP = $\beta_0 + \beta_1$ Treatment + β_2 Phase + β_3 Treatment:Phase + β_4 FoliageCover2 + β_5 FoliageCover3 + β_6 NestType + β_7 CPA + β_8 Replicate 2 + β_9 Replicate 3 + β_{10} Phase:NestType

180
	Control	Treatment
Phase 0 (before cull)	(β ₀)	$(\beta_0 + \beta_1)$
Phase 1 (after cull)	$(\beta_0 + \beta_2)$	$(\beta_0 + \beta_1 + \beta_2 + \beta_3)$

 Table S1. Using addition of logs to calculate In expected odds of ANP for phase, treatment and phase:treatment interaction, assuming constant values for other model variables

To calculate the Treatment: Phase effect:

i. Calculate relative change in ln expected odds of ANP before and after the cull in treatment and control sites respectively:

Relative change in expected odds of ANP = <u>Expected odds after cull</u> <u>Expected odds before cull</u>

ii. Calculate the relative difference between the change in expected odds of artificial nest predation in treatment and control sites to show effect of treatment:phase interaction:

Relative difference between change in expected odds in

treatment and control sites = <u>Expected odds after cull</u> (Treatment) <u>Expected odds before cull</u> (Control) <u>Expected odds before cull</u> (Control)

$$= \frac{\frac{\exp\left(\beta_0 + \beta_1 + \beta_2 + \beta_3\right)}{\exp\left(\beta_0 + \beta_2\right)}}{\frac{\exp\left(\beta_0 + \beta_1\right)}{\exp\left(\beta_0\right)}} = \exp\left(\beta_3\right)$$

Worked example (using best model):

Table S2. Model output

Predictor	Coefficient estimate (logit link)
Intercept	1.34
Treatment	0.04
Phase	-0.48
Treatment:phase	-0.32

	Control	Treatment
Phase 0 (before cull)	1.34 (3.84)	1.34 + 0.04 = 1.38 (3.97)
Phase 1 (after cull)	1.34 - 0.48 = 0.86 (2.36)	1.34 + 0.04 - 0.48 - 0.32 = 0.58 (1.79)

Table S3: Calculating In expected odds ANP by treatment and	
phase using addition of logs (with exponentiated value	s
in brackets) (see Figure 2(a), main document)	

Changes in expected odds of ANP due to effects of, respectively, Treatment, Phase and Treatment:Phase interaction (using back-transformed coefficients):

Change in Treatment sites = (Treatment, Phase 1)/ (Treatment, Phase 0) = 1.79/3.97 = 0.45 (55% decline)

Change in Control sites = (Control, Phase 1)/(Control, Phase 0) = 2.36/3.84 = 0.61 (39% decline)

Ratio of change in Treatment to change in Control = 0.45/0.61= 0.74

(see Figure 2(b), main document)

Table S4. Model parameters used in best model as predictors of odds of artificial nest predation.

Effect size and uncertainty (95% confidence intervals) are shown for fixed effects. Random effects were not included as they did not improve model fit. Note i) due to the logit model's log link function, original model output gives coefficient estimates for the log of the dependent variable. In this table, values have been back-transformed (see worked example above). Hence, for categorical variables, coefficient estimates represent the relative change in expected odds of ANP for a change from the reference level of the corresponding explanatory variable. For the continuous variable CPA, the coefficient estimate represents the relative change in expected odds of ANP for a unit change in CPA.

Fixed effects (back-transformed)	Coefficient estimate (back- transformed)	Lower confidence interval	Upper confidence interval
Intercept	3.84	2.08	7.08
Treatment	1.04	0.57	1.87
Phase	0.62	0.33	1.16
Treatment: Phase	0.73	0.33	1.61
Nest type	0.06	0.03	0.12
Phase:Nest type	4.22	1.81	9.82
Foliage cover 2	0.59	0.38	0.92
Foliage cover 3	0.26	0.11	0.62
CPA	0.75	0.61	0.92
Replicate 2	0.52	0.32	0.84
Replicate 3	0.63	0.39	1.01

		,	
Model	AIC	ΔΑΙΟ	No. of variables
Base + CPA + Foliage cover + Nest type + Replicate + Nest type:Phase	622.7	0.0	8
Base + CPA + Foliage cover + Nest type + Other predator density + Replicate + Nest type:Phase	623.1	0.4	9
Base + CPA + Area + Foliage cover + Nest type + Other predator density + Replicate + Nest type:Phase	623.7	1.0	10
Base + CPA + Area + Foliage cover + Nest type + Other predator density + Total stems + Replicate + Nest type:Phase	623.9	1.2	10
Base + CPA + Area + Foliage cover + Nest type + Replicate + Treatment + Nest type:Phase	624.1	1.3	9
Base + CPA + Foliage cover + Other predator density + Nest type + Replicate + TWI + Nest type:Phase	624.5	1.8	10
Base + CPA + Nest type + Other predator density + Noisy miner density + Replicate + Treatment + Nest type:Phase	624.7	2.0	10
Base + CPA + Foliage cover + Nest type + Replicate + Total stems + Nest type:Phase	624.8	2.1	9

 Table S5. Summary of best candidate models produced by the R package MuMIn which included the BACI base model (Treatment, Phase, Treatment:Phase).

Table S6. Coefficients for Firth logistic regression (with 95% confidence intervals).

	Coefficient	Lower confidence interval	Upper confidence interval
Intercept	2.08	0.20	3.96
Treatment	2.62	-2.76	7.99
Phase	0.55	-2.02	3.12
Treatment:Phase	3.02	-35.68	41.73

Chapter 5: Native to nemesis: a cultural history of the noisy miner

Statement of Contribution

This thesis is submitted as a Thesis by Compilation in accordance with <u>https://policies.anu.edu.au/ppl/document/ANUP_003405</u>

I declare that the research presented in this Thesis represents original work that I carried out during my candidature at the Australian National University, except for contributions to multiauthor papers incorporated in the Thesis where my contributions are specified in this Statement of Contribution.

Title: Native to nemesis: a cultural history of the noisy miner

Authors: Richard Beggs

Publication outlet: Australian Zoologist

Current status of paper: under review

Senior author or collaborating authors endorsement:

Richard Bezzy

Foreword

Chapters two, three and four reported on the empirical element of this study. Chapter five presents a cultural history of the noisy miner. Early in my research I encountered historical references to the species which expressed great affection. Such affection contrasts strongly with current negative sentiments towards noisy miners. This chapter charts the changes in attitude to the species since European settlement of Australia in 1788 and links this to the changing ecological impacts of the species as they have responded to anthropogenic habitat modification.

Abstract

1878: "gallant little birds" (Wagga Wagga Advertiser)

1915: "the carol of the magpie is eclipsed by the song of the miner" (Emu)

2004: "the mafia of the bird world" (Australian Broadcasting Corporation)

2015: "I hate those f***in things" (RedditAustralia)

The public image of the noisy miner (*Manorina melanocephala*), a honeyeater endemic to eastern Australia, has been severely damaged in recent decades on account of its violent tendencies towards smaller woodland birds, many of them of conservation concern. Aggressive exclusion of small woodland birds from potential woodland habitat by noisy miners was declared a Key Threatening Process under Australian federal conservation law in 2014. Noisy miners and other woodland birds have been evolving together for millions of years, however, so the threat presented by the noisy miner now is unlikely to be due to a sudden change in the species' behaviour. Using historical records of the species during the European phase of Australian history, this paper attempts to trace the cultural trajectory of the species from popular native bird to nemesis of small birds. I present historical evidence of changes in distribution and abundance of noisy miners and link these changes to the loss, fragmentation and degradation of native woodland that has occurred in eastern Australia since the introduction of European agriculture.

5.1 Introduction

"Aggressive exclusion of birds from potential woodland and forest habitat by over-abundant noisy miners (*Manorina melanocephala*)" was listed as a Key Threatening Process in Australia under the Environmental Protection and Biodiversity Conservation (EPBC) Act in 2014 (Department of the Environment, 2014). Overabundant species are native organisms whose otherwise normal ecological activities, such as foraging, predation, competition and brood parasitism, exceed the carrying capacity of a given social-ecological system. The carrying capacity may be ecological (Caughley, 1981) or cultural (Ellingwood and Spignesi, 1986; Dubois *et al.*, 2017; Australian Geographic, 2018). The cultural carrying capacity is the upper limit of population density of an overabundant species accepted by human society due to non-ecological impacts such as nuisance effects. Whilst overabundant native species are now recognised as an ecological problem globally (Garrott *et al.*, 1993; Mendelssohn and Yom-Tov, 1999; Lunney, 2007; Livezey, 2010), the noisy miner is the first native Australian animal whose behaviour has been listed federally as a threatening process.

All four members of the endemic *Manorina* genus are noted for their aggression and complex social relations, noisy miners being the most aggressive of the genus (Mac Nally *et al.*, 2014). Australia has the most aggressive birds in the world, particularly among the honeyeaters, as a result of concentrated sources of plant carbohydrate that can be efficiently monopolised through aggressive competition (Orians and Milewski, 2007; Low, 2014). Competition for nectar between honeyeaters can be fierce. Gould described the (now critically endangered) Regent honeyeater *Anthochaera Phrygia* as

....the most pugnacious bird I ever saw (Gould, 1865, p527).

The singing honeyeater Lichenostomus virescens was described as

....an exceedingly pugnacious bird, fighting with birds frequently much larger than itself (Fawcett, 1894, p550).

Many of the larger honeyeaters will chase away smaller species of nectarivores and insectivores (Ford and Paton, 1976; Chan, 2004; Mac Nally et al., 2005). Aggressive exclusion of smaller woodland birds by noisy miners in modified landscapes is therefore a particularly extreme manifestation of a natural Australian tendency towards interference competition among some birds. The permanent, colonial territoriality of noisy miners in fragmented woodland, however, combined with extreme aggression, has been implicated in the chronic decline of a wide range of smaller woodland birds across eastern Australia (Dow, 1977; Grey et al., 1998; Ford et al., 2001; Maron et al., 2013; Howes et al., 2014). Such effects occur at noisy miner densities as low as 0.6-0.8 individuals/ha (Mac Nally et al., 2012; Thomson et al., 2015). The noisy miner is a medium-sized honeyeater weighing 70 - 80g(Higgins et al., 2001). Given that aggressive dominance in passerines is a function of weight (Ford, 1979; Mac Nally et al., 2005), their size advantage allows them to aggressively exclude almost all smaller woodland passerines. Their co-operative defence of territory means they also will tackle larger creatures. They have been recorded harassing 65 bird species, including such non-competitive species as waterbirds, but will also harass many other vertebrates, with the intensity of harassment ranging from simple alarm calls through to physical attack and fatal injuries (Dow, 1970; Dow, 1977).

Changes in the distribution and abundance of Australian birds as a result of anthropogenic habitat modification are well known (Barrett *et al.*, 1994; Mac Nally and Bennett, 1997; Recher, 1999; Ford *et al.*, 2001; Lunney *et al.*, 2007; Martin and McIntyre, 2007; Catterall *et al.*, 2010; Mortelliti and Lindenmayer, 2015). The noisy miner represents a special case, however, as some ecologists believe that, along with changes in distribution and abundance, it has also changed its behaviour. The noisy miner appears to have two density-dependent modes of social organisation and behaviour. Such a phenomenon has been reported for the congeneric and similarly colonially aggressive bell miner *Manorina melanophrys*, which at low densities is not colonially aggressive (Clarke and Schedvin, 1999). Noisy miners are believed to exist in more intact landscapes at low densities without impacting other species. Densities of 0.02 birds/ha were observed in intact eucalypt woodland near Armidale, north-east New South Wales (Ford, 1985); 0.01 birds/ha were observed in young regrowth eucalyptus forest in south-east Tasmania and 0.05 birds/ha in mature forest in the same region (Taylor *et al.*, 1997); 0.33 birds/ha were observed in

Bennettswood, Victoria (habitat type not identified) (Higgins *et al.*, 2001). These studies do not, however, report on competitive behaviour of noisy miners. It may be that at low densities, noisy miners are less inclined to aggressively exclude other species because they lack the advantage of co-operative defence of territory. Alternatively, these two different modes of social organisation and behaviour may be dependent on resource dispersion inherent in vegetation configuration, and the consequent efficiency of defence. Noisy miners become an ecological problem in environments suitable for colonisation and collective aggression against other birds. The species is most likely to colonise woodland and forest edges and small (<300ha) fragments of productive eucalypt woodland with simple vegetation structure and connectivity to other patches, and (Maron *et al.*, 2013; Thomson *et al.*, 2015).

In modified landscapes that suit their habitat preferences, noisy miners interact aggressively with, and can have negative impacts on, a wide range of other woodland bird species (Maron *et al.*, 2013). Small woodland birds are already one of the most threatened groups of Australian birds (Paton and O'Connor, 2009; Ford, 2011a). Eighty per-cent of the temperate woodlands of south-eastern Australia have gone, with local losses as high as 95% (Hobbs *et al.*, 1993; Robinson and Traill, 1996; Olsen *et al.*, 2005). Declining habitat availability due to such habitat loss, and associated fragmentation and degradation, has created proportional declines in some small woodland birds with a number now threatened, endangered or critically endangered and a possible extinction debt still to be paid (Connor and McCoy, 1979; Woinarski *et al.*, 2006; Ford *et al.*, 2009; Paton and O'Connor, 2009) (but see Rayner *et al.*, 2014). Hence, the same habitat changes that have fostered the increased abundance of noisy miners also threaten many small woodland birds. By further excluding small woodland birds from potential habitat remnants, noisy miners are a threat multiplier.

The rise of the noisy miner from aggressive honeyeater to dominant species on a sub-continental scale is inseparable from the wider environmental changes that have occurred in eastern Australia since European settlement. Like many ecological problems, the changes in woodland bird assemblages due to the intersection of habitat modification and noisy miner behaviour, are not discrete, unconditioned events appearing spontaneously at a moment in time. They gestate slowly and often in a non-linear fashion, a product of the interaction of ecological processes and human intervention occurring at multiple spatial and temporal scales. Ecological communities characterised by strong interspecific interactions, such as avian assemblages in Australian woodland, are especially susceptible to threshold dynamics (Suding and Hobbs, 2009). As with the impacts of colonial aggression by noisy miners, tangible symptoms may not appear until long after their socialecological drivers first developed. In a prescient commentary on the expansion in range of the noisy miner in late 19th Century Tasmania, lawyer, naturalist (and avowed assimilationist) Morton Allport noted in an address to the island's Royal Society in 1867

> ... the well-being of living creatures in their wild state often hangs upon a very slender thread, and that in such case, but a slight alteration in the balance already established by nature may produce effects infinitely greater than anyone would be, at first sight, prepared to admit (Allport, 1867, p10).

Changes in the Australian environment since the time of Morton Allport constitute more than "a slight alteration in the balance already established."

5.1.1 Noisy miners and landscape transformation

The genesis of the noisy miner problem spans two distinct social-ecological phases in eastern Australia's natural history, the European and the pre-European. These two phases have had very different impacts on ecosystems in line with their respective scales and degrees of congruence, *sensu* Lindenmayer (2000), with natural ecosystem processes. Indigenous land management, principally the use of fire, occurred over as much as 50 000 years (Roberts *et al.*, 1990). This form of land management, combined with natural biotic and abiotic processes, also including fire, had a role in maintaining the variegated landscape encountered by Europeans in 1788 (Benson and Redpath, 1997; Bowman, 1998; Hateley, 2010). This variegated landscape would have contained a range of different vegetation configurations, including areas of woodland and forest of different stem density and different levels of shrub cover (Hateley, 2010), some of which may have approximated the vegetation configuration of remnant woodland patches which today are colonised by noisy miners.

Numerous early chroniclers referred to the presence in the eastern Australian landscape of what they termed "parkland," scattered trees with a grass understorey (Bonyhady, 2003). The first account was written 18 years before the First Fleet landed. Sydney Parkinson was a young artist and diarist on the Endeavour during James Cook's first voyage² (without which the First Fleet would probably never have sailed, at least not to Australia). Parkinson had been employed by Joseph Banks to

² Parkinson did not survive the voyage, dying at sea of dysentery contracted in Java, though his name lives on in the Parkinson's or black petrel, *Procellaria parkinsoni*.

draw botanic samples. Sailing close to the coast of what is now central New South Wales, his entry for 27th April, 1770 represents an early example of ecological assessment by remote sensing:

The country looked very pleasant and fertile; and the trees, quite free from underwood, appeared like plantations in a gentleman's park. (Parkinson and Kenrick, 1773, p134).

Many other early accounts of the colony noted the presence of open grassy woodland. Within five years of the establishment of the first penal settlement at Sydney Cove, Watkin Tench had described the landscape of open woodland encountered by the first party to explore westwards from Sydney Cove towards the mountains:

> the face of the country is such, as to promise success whenever it shall be cultivated, the trees being at a considerable distance from each other, and the intermediate space filled, not with underwood, but a thick rich grass, growing in the utmost luxuriancy (Tench, 1793, p37).

Cunningham, one of the first writers to relate vegetation to soil type, wrote in 1827 of

... a fine timbered country perfectly clear of bush through which you might....drive a gig in all directions without any impediment (Cunningham, 1827, p77-78).

This same distinction between open woodland and denser forest was made by naturalist George Caley in his account of the exploration of the Blue Mountains in 1804 (Andrews, 1984). He referred to the denser areas as brush, which, as with Cunningham's "bush" above, suggests a shrubby understorey as distinct from mature trees. Unfortunately, the historical nomenclature causes confusion today as the colonial term for impenetrable forest was "brush" whilst "forest" meant country sufficiently open and grassy to permit grazing (Bonyhady, 2003). The possibility of movement through such open woodland was repeated by Charles Wilkes during a US exploration of Australia in 1839. Like Cunningham, he noted that the "forests" of New South Wales were so open that

.... a carriage may be driven rapidly through them without meeting any obstruction (Wilkes, 1845, p178).

Such early references to "parkland" and open grassy woodland free of a shrubby understorey are significant, as such vegetation structure conforms in outward appearance to the vegetation type today colonised by noisy miners (Grey *et*

al., 2011). Firm conclusions about the scale of the different elements of landscape structure cannot be drawn simply from contemporary accounts, however (Clark, 1990; Dovers, 2000; Bowman, 2001). The fact that areas of open grassy woodland existed tells us little of how the landscape was partitioned between the different vegetation types. Indeed, early colonists would have been particularly attracted to landscapes ready for grazing with minimal clearing. This attraction may partially explain the recurrence of reports of grassy open woodland in the early colonial period. In addition, given the biotic and abiotic transformations that have occurred in eastern Australian agricultural landscapes during the colonial period, it is impossible to say with certainty whether noisy miners would have colonised suitable areas in the way seen today, but it is not implausible.

Similarly, taking historical landscape paintings as true and representative depictions of contemporary Australian landscapes has its critics (Doherty, 2013). There have been suggestions that some colonial painters interpreted the landscape through the lens of European cultural expectations or even personal melancholia (Hackforth-Jones, 1977). Indeed, pastoral art during the Romantic period of the late 18th to mid-19th Century was based on creating attractive images of an idealised natural landscape. In Australia, such an approach would have fitted in with the idealised rural narratives of the squatter, the selector and the "sheep's back." The pastoral landscapes of Arthur Streeton, Hans Heysen and Tom Roberts

... shaped the way Australians viewed the landscape andbecame for a largely urban population the quintessential image of the Australian bush (Yates and Hobbs, 2000, p3).

Nevertheless, many of the landscapes that colonial artists painted showed a variegated configuration of patches of grassland, open grassy woodland and denser areas of forest (see Figures 8 - 11, Appendix). Hence, the artistic record generally supports the written accounts of early chroniclers and suggests that at least some of the pre-colonial landscape could have supported noisy miner colonies.

The pre-European phase was followed by two centuries of the application of European agricultural methods to the Australian environment. Deforestation was the most ecologically dramatic in a disturbance regime which included changed hydrological, nutrient and fire regimes, introduction of invasive species and destruction of native predators (Hobbs and Hopkins, 1990; Glanznig, 1995; McIntyre *et al.*, 2004; Lindenmayer and Burgman, 2005).

We know what the ecological impacts of the noisy miner are now, and we have a good understanding of the role of vegetation structure in determining noisy miner colonisation (Maron et al., 2013; Thomson et al., 2015). My hypothesis is that prior to the European phase, noisy miner aggression structured avian assemblages at a local scale in open woodland habitat suitable for noisy miner colonisation. It seems unlikely that noisy miner competition was a threatening process at this time. Smaller woodland species vulnerable to noisy miner aggression could simply have chosen to inhabit areas of woodland where noisy miner density was low. If current noisy miner habitat preferences applied prior to European colonisation, then some of the woodland in the variegated landscape that existed at that time would have been unsuitable for noisy miner colonisation, due, for example, to a shrubby understorey. There would, therefore, have been alternative habitat for small woodland birds, unlike in modern, noisy miner-dominated, modified landscapes. What proportion of the pre-European woodland landscape was suitable for noisy miner colonisation, and what proportion would have supported populations of small woodland birds, is unknown. The key to the development of noisy miner competition into a threatening process for small woodland birds is the intersection of co-operative noisy miner aggression and limited alternative habitat for small woodland birds.

The first scientific account of the development of a potential ecological problem due to noisy miner competition appeared in 1977 (Dow, 1977). At some time between 1788 and 1977, therefore, natural noisy miner aggression became a threatening process for small woodland birds already impacted by habitat modification. How this problem developed temporally and spatially is unknown. If it was driven by habitat modification, then it is likely that it occurred at different periods in different places according to local levels of landscape modification.

This chapter has two purposes. The first is to present a historical narrative of the place of noisy miners in the eastern Australian environment. Through a review of historical references to the species, this part of the chapter develops a putative historical trajectory of the evolution of noisy miner ecology from one aggressive honeyeater in a gallery of potential violent offenders, to a significant ecological problem. I attempt to identify where and when such ecological changes occurred and seek evidence for my hypothesis that noisy miners were not a threatening process prior to the European phase. I focus on evidence of changes in distribution, abundance and behaviour of noisy miners.

The paper's second purpose is to consider the cultural attitudes to noisy miners expressed through the historical narrative. Current cultural attitudes to the species are dominated by considerable antipathy (Lambert, 2016b). Scientific studies of the species use descriptors such as "despotic", "hyperaggressive" and "bully" (Mac Nally *et al.*, 2000; Piper and Catterall, 2003; Hastings and Beattie, 2006; Maron *et*

al., 2013; Howes *et al.*, 2014; Loyn *et al.*, 2016). In informal settings I have heard ecologists compare the species to "a plague" and "a cancer." Some expressions of personal sentiments towards the species in popular online media are even less restrained (Aussie Finch Forum, 2012; RedditAustralia, 2015). Such sentiments contrast sharply with the great affection for the species expressed in some historical references. Based on this contrast, I posed three research questions:

- i. Is there evidence in the historical record of a change in cultural attitude to noisy miners?
- ii. Is there evidence in the historical record of a change in noisy miner abundance, distribution or behaviour?
- iii. Is there evidence in the historical record that changes in cultural attitudes reflect a change in the species' ecological role?

From preliminary investigation, I knew that the cultural attitude expressed in some historical records contrasted strongly with current negative views of noisy miners. My expectation was that, through further consideration of historical accounts, a clear picture would emerge of a gradual change in cultural attitude.

In the post-war period, noisy miner abundance has increased across the species' range, with reporting rates in some areas increasing by 10 to 15% between 1984 and 2002 (Barrett *et al.*, 2007). Localised changes in distribution have also been recorded in recent decades, particularly in urban areas (Officer, 1964; Lindsey, 1985; Barrett *et al.*, 2003; Catterall *et al.*, 2010). Systematic evidence of changes in abundance and distribution of noisy miners is unlikely to exist in the historical record, however, because systematic surveys were not conducted until recent decades. Nonetheless, given that noisy miner colonisation is largely determined by vegetation structure at patch and landscape scale (Maron *et al.*, 2013), I expected to find anecdotal evidence of local changes in abundance and distribution as habitat modification created new opportunities for noisy miner colonisation.

My belief is that noisy miners have always been colonially aggressive in suitable habitat, but that such aggression has only become a threatening process to small woodland birds in the European phase due to a decline in availability of noisy miner-free woodland habitat. Since the noisy miner is such a vocal and active aggressor, I expected to find accounts of its aggressive tendencies in the historical record. I also expected to find accounts of its local impacts on small woodland birds in more recent references.

5.1.2 Miner, minah or myna? A note on the confusions of taxonomy

The noisy miner has had many different common and scientific names through the European period, which complicates any attempt at a representative search of historical records. John Latham, the so-called "Grandfather of Australian ornithology" (Encyclopaedia of Australian Science, 2019) unwittingly gave the species four separate scientific names, believing each to be a separate species (Latham, 1802; Salomonsen, 1967). He can perhaps be forgiven, for he never set foot in Australia, working only from bird skins and paintings sent back on a long sea voyage. Latham's name lives on in the accepted scientific names of many Australian birds. The current *Manorina melanocephala* (Latham) is the last in a long list of scientific names applied to the noisy miner by taxonomists (Schodde, 1999).

Like many well-known Australian birds, the noisy miner has had multiple common names (Barrett, 1946). In most early historical references it is called the *soldier-bird* eg (Howitt, 1845). Historical sources attribute this name variously to the species' aggressive behaviour towards competitors or predators, its habit of "going about in companies" and its "erect bearing" ("Platypus", 1941; Anon, 1947). Howitt considers "soldier-bird" appropriate on account of the species guard-like behaviour:

It is the very sentinel of the woods, sending far on before you intelligence of your coming (Howitt, 1845, p142).

It is also called the *snake-bird* because it is "particularly noisy when it sights a snake" (Anon, 1947). Other names include *squeaker* and *Mickey miner* (Gray and Fraser, 2013). *Miner* and *myna* derive from the Hindi word for starling, *maina* (Morris, 1898; Gray and Fraser, 2013). The often-confused common or Indian myna *Acridotheres tristis*, which has become invasive in Australia since its introduction to Victoria between 1863 and 1872 (Barrett, 1946; Hindwood, 1947) is, taxonomically, a starling. A form intermediate between miner and myna was applied to the noisy miner in an account of Van Diemen's Land (never colonized by the Indian myna) three decades before the introduction of Indian mynas to mainland Australia:

The restless and noisy minas are disputing amidst the bright yellow blossoms of a neighbouring wattle (Henderson, 1832, p41).

Given the similarities in size, communal behaviour, loud vocalisations, yellow beak, eye-skin and legs, and a partial ground-foraging habit, it is unsurprising that colonists or explorers already acquainted with the Indian myna in British Asia, would draw a comparison with the native noisy miner. Once the Indian myna had been introduced into Australia, and the name "miner" applied to the noisy miner, confusion between the two species was almost inevitable and continues to the present (O'Shaughnessy, 1995). Another intermediate form, minah, appears in 1877 in a description of rural Victoria:

...yellow-legged minahs, tamest of all Australian birds, fly into the big farm kitchen where even the chickens dare not venture, and pick crumbs from the earthen floor (Macdonald, 1887, p146).

The adjective "Australian", along with a mention of the "Indian minah" as a separate species elsewhere in the same reference (p72), confirm that the species in question is the noisy miner.

The modern form *miner* first appears in Gould (1848) whilst the first published use of the full name *noisy miner* is in Lyons (1901). That reference describes a journey in the Lake Eyre region, so the author is mistakenly referring to the yellow throated miner, *Manorina flavigula*.

5.2 Methods

5.2.1 The historical narrative: a review of historical references

Given the long timescale over which the noisy miner has inhabited Australia's changing ecosystems, an environmental history approach lends itself to any study attempting to work out a trajectory of such changes. Environmental histories are beset with uncertainties of a different degree to scientific studies (Clark, 1990; Dovers, 2000; Bowman, 2001). In this chapter I aim to reduce the degree of uncertainty surrounding the history of the noisy miner by combining current ecological knowledge of the species with historical references. Historical references to the noisy miner cover a long period of habitat modification. Whilst such references are low resolution and not systematic, they are the only records we have of how distribution, abundance and behaviour of the species may have changed, and of any shift in cultural attitudes to the species. Changes in cultural attitudes to particular species may reflect changes in society's values, or changes in the ecological role of the species, or both (Lunney and Leary, 1988; Lunney, 2001; Carruthers and Robin, 2010; Carruthers *et al.*, 2011). One of the aims of this chapter is to determine which case applies to the noisy miner.

Environmental histories sometimes use historical records of particular organisms created as a result of economic or social needs to estimate abundance of the organisms. Thus records of hunting success of macropods subject to bounties represent a crude measure of relative abundance (Jarman and Johnson, 1977). Noisy miners were frequently cited as an agricultural pest in the 19th Century. "Bonuses" were offered by a Noxious Birds Destruction Society at Bulga, NSW, for the heads of a range of birds, including the noisy miner (Anon, 1892). A penny was offered for each "soldier-bird" destroyed³ but I was unable to find a record of numbers delivered. Due to the lack of records, it is difficult to provide numerical estimates of noisy miner abundance in the pre-colonial and early colonial periods. The only comparison that one can make is with current records of noisy miner density in more intact woodland, at 0.01 - 0.07/ha (Higgins *et al.*, 2001).

The historical narrative presented in the chapter is based on a review of historical references to the noisy miner with particular attention to the cultural attitude expressed in them. Such references include observations of behaviour, records of changes in distribution and notes on economic impacts. These references were collated from newspapers, government reports and articles in scientific and ornithological journals. Over 3500 references to the species from 1792 to the present were encountered on the National Library of Australia's online archive, Trove.

5.2.2 Changing cultural attitudes to noisy miners: a semi-systematic review of historical references

Such a non-systematic review of historical references risks bias towards the more interesting records of the species and records whose cultural attitude contrasts most strongly with modern antipathy. I therefore also completed a semi-systematic review of newspaper articles. I chose newspapers because I considered them a useful indicator of cultural attitude to the species and because there is a continuous record of digitised newspapers from 1840 to 1999 in the Trove archive. Newspaper content included articles, letters, children's stories, anecdotes, poems and references to government publications. The content of these references was subjectively classified into one of three categories, positive, neutral or negative, according to the underlying cultural attitude expressed. I used the affective tone of sentiments towards the species as an indicator of cultural attitude. Examples of positive sentiments include expressions of affection for the species or its behaviour, or an appreciation of some positive role played by the species such as the habit of loudly indicating the presence of snakes or its consumption of forestry insect pests. Negative sentiments include the species' role as an agricultural or urban nuisance or pest, or references to its ecological impacts. Neutral attitudes generally appear in factual accounts of the

³ For comparison, flying foxes, also included in the list of noxious birds, received threepence per head.

species or its behaviour, with no indication of an underlying sentiment towards the species.

5.2.3 Search methodology

In my Trove search term I included all known common names of the species. I refined my search as much as possible to exclude references to sport (there was a racehorse called Soldierbird in Victoria in the 1880s and 1890s) and the mining industry. Nevertheless, some "noise" was inevitable in my final count of references for each decade. Snake-bird, for example, was also a common name for the darter *Anhinga novaehollandiae* and soldier-bird sometimes referred to the apostlebird *Struthidea cinerea* (D Paton, pers. comm. 2017, University of Adelaide) or the noisy friarbird *Philemon corniculatus* (Fawcett, 1894). Where Noisy Miners and noisy friarbirds appeared in the same reference, as, for example, in an account by one of Leichhardt's companions (Bunce, 1856), the distinction was usually clear from the context or because the noisy friarbird's other common name, *leather head*, was also used.

The refined search for the semi-systematic review gave a list of more than 2000 references. For each decade, I let Trove sort by "relevance" of the reference to search terms rather than date so that references were sorted randomly with no bias towards the beginning or end of a decade. My sample consisted of the first ten references for each decade which unequivocally referred to noisy miners. This yielded a total of 125 references for the 16 decades as not all decades had ten suitable references. Once a reference was included in my classification, I excluded syndicated versions of the same reference in other newspapers. Where the reference simply used a characteristic of noisy miners to provide a familiar comparison with other species (e.g. size, nest type), I did not use the reference. My prediction was that, over the period sampled, this semi-systematic review would show an increase in the percentage of articles displaying negative cultural attitudes to noisy miners and a decline in the percentage of articles displaying positive cultural attitudes.

5.3 Results and discussion

5.3.1 A cultural chronology of noisy miners

5.3.1.1 Indigenous antecedents

Noisy miners were known to indigenous peoples in parts of New South Wales as *cobaygin* (Gould, 1848), in Victoria as *pootch* (Anon, 1870) and in the Blue Mountains as *que que gang* (Koch, 2009). The Wurrung dialects of south-western Victoria have a number of names for the species including *putj, tuwitj, purpur* and *pirndiyn* (Wilson et al., 2017). As *Deegeenboyah*, the species was a character in indigenous stories ("Aunt Patsy", 1922) and in a Wurrung creation myth in which ancestor *Murkupang's* dingoes turn themselves into birds, one dingo becomes a noisy miner (Mathews, 2007). An article in a 1917 edition of the *South Australian Ornithologist* about the alarm call emitted by noisy miners in response to raptors, noted

....the aborigines used to make use of an imitation of this alarm call to bring high flying ducks to the water and within range (Anon, 1917, p55).

The loud alarm calls of noisy miners represented an irritating disturbance for indigenous as well as white Australian hunters (Campbell, 1894):

An old settler in the Western district used to relate how angry the minah made the blacks by chattering over their heads when they were stalking prey. Their exclamation was, "Minah big rogue; always tell on black fellow." (Campbell, 1894, p29).

5.3.1.2 The first 150 years after invasion

Noisy miners were present in the wooded areas of Sydney Cove in 1788 for, in the first decade after the arrival of the First Fleet, two annotated paintings were made of the "chattering bee-eater," one of six early names given to the species by taxonomists. The paintings make up items 96 and 97 of the bird series of the Watling Collection, a wildlife series now in the First Fleet Artwork Collection of the Natural History Museum, London (Hindwood, 1970). In 1801 the paintings of birds in the series (or, possibly, copies of them), were catalogued by John Latham (Hindwood, 1970). One of the two noisy miner paintings (Figure 1) was by Watling himself, a trained artist and convict forger from Dumfries in Scotland. The other painting was anonymous, and both are accompanied by handwritten annotations which include the following observation of noisy miner behaviour:

It is pretty numerous and always at war with others of the feathered tribe (Anon, 1792).

In an echo of the irritation expressed by indigenous hunters above, the annotation also included the phrase

This chattering Bird often gives notice to the Kangaroo when the Sportsmen are after them (Anon, 1792).



Figure 1. Watling's "Chattering Bee-eater," 1788-1792 (By permission of the trustees of the Natural History Museum (London))

Under the name *Myzantha garrula*, Gould gives the earliest indication of the original distribution of noisy miners through

...Van Diemen's Land and all parts of the colonies of New South Wales and South Australia...(Gould, 1848, p169),

adding Victoria in his 1865 Handbook of Australian Birds (Gould, 1865).

Articles about the noisy miner were particularly prevalent in east coast newspapers in the late 19th Century and into the 20th Century (Figure 2), many of them syndicated through local papers across the eastern states. Some articles considered the noisy miner a loveable garden visitor or described its behaviour or the characteristics of its nest and eggs in a "nature notes" format. Others indicated its potential as an agricultural pest. "Notes of the month" in the Illustrated Sydney News of February 1854 reported that

The orchard fruits are ripe, and several species of birds are committing sad havock. Among these we recognise the Soldier Bird (Myzantha garrula), a noisy active little creature.... (Anon, 1854, p2).

In March 1860 the Sydney Morning Herald repeated the accusation (Anon, 1860b), while the Maitland Mercury in February 1863 described the species as



Figure 2. Incidence of Australian newspaper articles 1840-1999 containing "soldier bird," "mickey miner", "snake bird" or "noisy miner"

.....the greatest pest to the vine grower (Anon, 1863, p8).

Further references to the soldier-bird's effects on fruit production appeared in newspapers in 1886 and 1896 (Forbes, 1886; Anon, 1896). In contrast, a horticulturalist presented a paper to the First Intercolonial Convention of Fruit Growers in 1894 in Victoria in which he acknowledged the important role of birds such as the noisy miner in biological control of insect pests in orchards and stated of the noisy miner

I do not put him down as a very momentous drawback to fruit culture in Mildura (Fletcher, 1894, p5).

A similar sentiment was expressed in the Adelaide Advertiser in 1932:

.... It must not be forgotten that the Noisy Miners also feed on orchard pests and make it possible for the gardener to grow fruit ("Galah", 1932, p14).

In March 1878 the Sydney Morning Herald reported on a debate in the New South Wales Legislative Council regarding the introduction of a game protection bill. The article noted that the noisy miner was "very destructive to some kinds of crops" (Anon, 1878a). It was therefore proposed in the bill that the species be excluded from protection. Later, along with almost 40 other native and introduced species, the noisy miner was listed as an unprotected bird under the New South

Wales Animals Protection Act 1918 (Government Gazette of the State of New South Wales, 1921). These reports are anecdotal but they suggest that by this time the population of noisy miners was well-established in the agricultural landscape. An article in the Melbourne Argus in 1912 stated

In New South Wales and parts of Victoria, the minah is probably the most common of all birds (Sherrie, 1912, p7).

Support for shooting of the birds was by no means universal. A writer in The Sydney Mail and New South Wales Advertiser in July 1878 noted the value of the bird's habit of gleaning insects from bark⁴:

The proprietors of ornamental and other valuable timber plantations, as well as those who cultivate gardens, should befriend the soldier bird as the natural enemy of several kinds of wood-boring beetles that both in the perfect and larva state play havoc amongst the leaves, roots, and branches of forest and other trees (Pinion, 1878, p135).

The capacity of noisy miners to warn people of the presence of snakes seems to have elicited some affection amongst the population. An article in the Wagga Wagga advertiser in 1878 (and syndicated through several regional newspapers) noted "the determined antipathy shown by the soldier bird to the snake" and continued,

> A gentleman proceeding along the Goulburn road, on horseback, had his attention attracted by the noisy commotion of a number of soldier birds in Cunningham's paddock Between twenty and thirty of the gallant little birds were darting down and pecking at a large brown snake, which was up on end parrying the attack of its tormentor (Anon, 1878b,

рЗ).

An example of the danger of relying on individual historical sources, however, is provided by the Austrian naturalist, Georg Frauenfeld. Following his 1858 trip to Australia, he presented his findings to the Mathematical-Scientific Section of the Imperial Academy of Sciences, Vienna, asserting that

the Common Soldier Bird is highly valued by all settlers for consuming poisonous snakes (Frauenfeld, 1859, p1).

⁴ More recently noisy miners have been implicated in insect dieback of trees, possibly due to exclusion of small insectivores from woodland patches (Ford and Bell, 1981; Ford, 1986; Loyn, 1987; Clarke *et al.*, 1995; Grey *et al.*, 1997).

Other than its role as an agricultural pest, many of the historical references during this period indicate public affection for the species. The third verse of Henry Lawson's unpublished⁵ 1909 poem "The Soldier Birds" relates the bird to nostalgia for childhood, as well as indicating the species' association with human environments:

I mind the blue-grey gully bush The slab-and-shingle school, The "soldier-birds" that picked the crumbs beneath the infants' stool (Coleman, 1933, p9).

Whilst soldierbird has also been used to refer to apostlebirds (D Paton, pers. comm. 2017, University of Adelaide), the final verse clarifies the species in question with a reference to "the little grey-clad soldierbirds." Further confirmation of their identity is given in an article in the NSW Public Teachers Federation magazine, 1933, in response to an article about the poem in the Sydney Morning Herald published the same year, where the writer refers to them also as "minahs" (Stone, 1933). A further five poems published in newspapers between 1893 and 1918 included mention of "soldierbirds" and, like Henry Lawson's poem, entailed romantic depictions of the pastoral idyll.

In 1911, a "Soldier Bird Club" was set up at the school in Sutton Forest, New South Wales with the intention of encouraging pupils to put out food for them (Carter, 1911). Four years later an article entitled "Morning Song of the noisy miner" appeared in Australia's oldest ornithological journal, *Emu*, eulogising the dawn chorus of the species:

Before sunrise, and as the day breaks, a solitary bird will pour forth for twenty minutes a most agreeable song in its nesting area... I think the carol of the magpie is eclipsed by the song of the Miner (Hall, 1915, p185).

In an impressive display of deep listening, the author transcribed the song in musical manuscript, complete with lyrics and dynamics (Figure 3). Similar sentiments were expressed in *The Land* a few years later

in the early morning they sing a joyous and most melodious chorus—bringing into effect notes of a quality which are not heard at a later hour in the day (Sherrie, 1917, p12).

⁵ The poem was reproduced in an article in the Sydney Morning Herald in 1933 (Coleman, 1933).



Figure 3. The morning song of the noisy miner (Emu, 1915)

The noisy miner's "beautiful clear call" was mentioned in the Adelaide Advertiser ("Galah", 1932) and the sentiment was repeated in a 1936 article in the *Farmer and Settler*:

An early riser, he sings a most attractive song, quite different from the shrill warning cry we hear later in the day (Kemmia, 1936, p15).

In discussing "The Woman's Bird", a recent arrival to the bush stated in a 1925 edition of the Australian Woman's Mirror

My vote would be cast for the grey-green and cheeky mickies or Noisy Miners I am full of gratitude to them, for I am sure they saved me from a nervous breakdown and helped me to learn to love the bush and its birds (B.F., 1925, p31).

5.3.1.3 The post-war period

Newspaper articles about noisy miners continued to appear in the post-war period, although less frequently (Figure 2), including the popular "nature notes" format offering descriptive accounts of the bird and its habits. The habitat preferences of the species were well known by this time, as was its adaptation to new forms of habitat such as roadside plantings and cleared areas. A 1946 article in the Hobart Mercury about "noisy honeybirds" noted that the birds

> ...assemble for their daily meetings and concerts in gum trees along country roads and the edge of forest clearings....(Anon, 1946, p6).

The Melbourne Argus reported in 1947 that

It is often found in small parties in open forest country, especially where the land has been partially cleared (Anon, 1947, p7).

A year later the Hobart Mercury stated

.....there are many districts where it never occurs because of the dense-ness of forest....("Peregrine", 1948, p9).

Details of the birds' complex co-operative breeding behaviour were unknown prior to the work of Dow (1970). The same article in the Hobart Mercury observed,

> ...there never seem to be as many nests as there are pairs in the Spring. The sociable birds will congregate in flocks of a dozen or more in given parts of the bush, but it would appear from the absence of nests that only a small proportion are actually breeding ("Peregrine", 1948, p9).

5.3.2 Changes in distribution and abundance

The rate at which noisy miners responded to the gradual increase in area of woodland suitable for colonisation is unknown. The first recorded reference to a change in their distribution is from 1867 when lawyer and naturalist Morton Allport presented a paper to the Royal Society of Van Diemen's Land (Figure 4). In his paper he noted the change in distribution of Australian magpies *Cracticus tibicen*, eastern rosellas *Platycercus eximius* and the noisy miner (then still referred to as *Myzantha garrula*). Hobart was founded in 1804 but, according to Allport, until "a few years"

ON THE LOCAL DISTRIBUTION OF SOME TAS, MANIAN ANIMALS.

BY MORTON ALLPORT, F.L.S., F.Z.S.

EVERY person who takes the slightest interest in our natural history must have observed many instances of local distribution, of birds especially, which are often unaccountable, but which, nevertheless, carry with them very useful lessons as to the difficulties of establishing new forms of animal life, in a country already occupied, without great danger to the original occupants.

Many of the Fellows of this Society must have noticed the absence (till lately) from our suburbs of the black and white or whistling Magpie (Gymnorhina organicum), the Miner (Myzantha garrula), and the Rosella parrot (Platycercus eximius). From the earliest days of Hobart Town till a few years ago, these three birds were unknown, as residents, on the Hobart Town side of the Derwent, from Glenorchy to the Huon, although much of the country lying between these places is apparently similar to that inhabited by the same birds at a distance. So marked was this absence in the case of the Magpie and Rosella that Mr. Gould, the celebrated ornithologist, specially refers to it in his recently published handbook on the birds of Australia.

Figure 4. The title page of Morton Allport's 1867 lecture to the Royal Society of Van Diemen's Land, the first documented reference to the changing distribution of the noisy miner

before 1867, noisy miners had not ventured into the town. Allport's commentary suggests that by 1867 they had expanded their distribution from the north and east into Hobart and a further 28km into the agricultural districts of the south and west as far as the river Huon (Allport, 1867). This commentary is an early indication of some of the species that have benefitted from habitat modification and which are now recognised as members of the "big bird assemblage" associated with noisy miners (Maron *et al.*, 2013).

Noisy miners were unknown in the Adelaide area until the early 1890s and in the early 20th Century their range expanded west from the Mount Lofty Ranges (Zietz, 1914b; Anon, 1917). Further expansion occurred in South Australia in the mid-1970s (Paton *et al.*, 1994a) and by the 1980s they were present through much of the state (Paton *et al.*, 1994b).

The northernmost extent of the noisy miner's range (here described with the scientific counterpart of the older common name *garrulous honeyeater*) at the end of the 19th Century appears to have been Herberton in the Atherton Tablelands in Queensland:

The soldier-bird, Manorhina garrula, occurs along the Herbert River, near Herberton, and on the Wild River, though it is somewhat scarce at the latter place. Its range is from the latitude of these places to Tasmania. It extends again inland for perhaps 200 miles, but beyond this limit is succeeded by an allied species, M. flavigula (Anon, 1894, p214).

In 1953, the species was recorded more than 250km further north at Fairview, 21km north west of Laura, in Far North Queensland (Storr, 1953). By 1963, noisy miners were observed more than 100km further to the north and west on the Cape York Peninsula (Officer, 1964). The New Atlas of Australian Birds (2003) reports noisy miners an additional 30km to the north. Changes in distribution also occurred in the Sydney region, the species being recorded in Beacon Hill for only the second year in 1983 (Lindsey, 1985).

There is considerable regional variation in changes in noisy miner abundance. The earliest record of localised increases was around Barrington in New South Wales (Hyem, 1936). As late as 1948, the species appeared not yet to have reached invasive proportions in Tasmania. A report in The Mercury stated,

> In numbers, the bird does not appear to do more than hold its own anywhere in the State. This static population may be due to a naturally low rate of reproduction or to mortality, of young and eggs... ("Peregrine", 1948, p9).

Lindsey (1985) records that noisy miners were "still increasing in the Sydney region, especially the city centre" and Morris (1986) notes increasing abundance of noisy miners in urban areas generally since 1975, listing noisy miners among a suite of species which had "increased markedly" in the Sydney metropolitan area. In 1972, in a letter to the Canberra Times, the noisy miner was listed as a common garden bird in that city (Edgar, 1972). Subsequently, populations of the species expanded in Canberra, with marked increases in reporting rate, frequency and abundance beginning in the early 2000s (Figure 5). A similar increase in abundance was observed in suburban Brisbane between the early 1990s and the mid-2000s (Catterall *et al.*, 2010), where noisy miners were found to thrive in suburban gardens where a eucalypt canopy persisted (Sewell, 1992). It is likely that urban habitat loss and fragmentation benefits noisy miners in a similar way to rural habitat modification due to agricultural development (Low, 1994). At the same time, planting of nectarrich native garden plants may have encouraged the species (Catterall, 2004).

Based on the situation in intact areas today, the natural density of miners prior to them becoming a problem in recent decades is thought to have been 0.01-0.07/ha (Higgins *et al.*, 2001). Their abundance has now increased over most of their range,



Figure 5. Changes in abundance, reporting rate and frequency of sightings of noisy miners in Canberra, 1982-2015 (Source: Canberra Ornithologists Group Garden Bird Survey) Abundance: average no. of birds observed for each period of observation (including all zero records). Reporting rate: percentage of records with any noisy miner observations. Frequency: percentage of all sites that had any observations of noisy miners

with densities of 7–10 birds/ha recorded in the 1970s, at the time the highest of any Australian passerine (Dow, 1978). Densities more than double that have been reported in the South West Slopes region of New South Wales (Beggs *et al.*, 2019). Reporting rates in some areas increased by 10% to 15% between 1984 and 2002 at the same time as woodland specialists declined (Barrett *et al.*, 2007). Analysis of survey data across 37 bioregions for the period 1998-2012 showed increases in noisy miner reporting rates in nine bioregions and declines in none (Maron *et al.*, 2013). Some of these increases were as high as 20%. In one area of New South Wales noisy miner densities increased by 100% between the mid-1990s and early 2010s (D. Oliver, unpublished data quoted in Maron *et al.*, 2013).

5.3.3 Changes in behaviour and a shift in cultural perceptions

Observations of noisy miner aggression against other species appear frequently in the historical record, starting with the first colonial era reference to the species in the annotation to Watling's painting completed soon after the arrival of the First Fleet (see *The first 150 years after invasion* above). In 1860, an article in the Sydney Morning Herald noted the aggressive defence of nests:

Magpies and soldier-birds are building their twig-formed nests, placed in the forks of trees, and growing very bold and pugnacious in their defence (Anon, 1860a, p2).

Describing the noisy miner as "one of our cheekiest little birds," an article in the Sydney Evening News noted that

It is constantly driving off other birds, pursuing them for a considerable distance, uttering its resistant cries the whole time ("Kurrajong", 1927, p8).

An article in *Emu* in 1956 is the first report of lethal aggression by noisy miners (McKenzie, 1956). The first record indicating that noisy miner aggression might be affecting bird assemblages was made in 1953 when Gannon noted that, along with the "Grey Butcher-bird, Red Wattlebird, etc", noisy miners are

.....birds that are aggressive to smaller birds and not good mixersso, no doubt...... have some bearing in limiting areas for the smaller birds to nest in (Gannon, 1953, p201).

Dow's work then showed unequivocally how noisy miner aggression excluded most small woodland birds from colonised areas (Dow, 1977). Since then there has been a rising output of academic studies as the extent of the problem has become more widely recognised (Figure 13, Appendix).

This recognition of the ecological impacts of noisy miner aggression appears to have been reflected in popular culture as expressed in newspaper reports, radio broadcasts and, especially, on the internet where unrestrained invective is frequently and freely expressed. Below is a selection of statements from these sources to indicate changes in our perception of noisy miners in recent decades compared to some of the positive sentiments for the species expressed in the 19th and early 20th Centuries:

Newspapers: "Scientists want Noisy Miner cull," "Noisy Miners form gangs..." (Peddie, 2011); "the gang tactics of Noisy Miners" (The Australian, 2014); "The birds we love to hate," (Lambert, 2016a).

Radio broadcasts: "indigenous pest," "the mafia of the bird world," (Clarke, 2004); "Native or not, it's time to cull Noisy Miners" (Taylor, 2016).

Online: "Noisy bullies" (Birds in Backyards, 2011); "Those Damn Noisy Miners…" (Aussie Finch Forum, 2012); "What I hate with a passion is the noisey minor [*sic*] birds" (Whirlpool, 2014); "Obnoxious little gangs" (No Award, 2015);

"I hate those f***in things" (RedditAustralia, 2015); "I absolutely categorically unequivocally and viscerally *hate* miner birds...... It's only a matter of time before I get a bb gun and go all Rambo on their feathery little asses" (comment on (Lambert, 2016b).)

5.3.4 Semi-systematic review of newspaper articles

The Trove archive returned 2474 newspaper articles from 1840 to 1999 containing the search terms (Figure 2). To put this in perspective, the same search for "magpie"⁶ returned almost 200 000 entries (Figure 12, Appendix).

I predicted that an increasing number of newspaper articles expressing negative sentiment towards the species would appear after the ecological impacts of noisy miner aggression became well known as a result of the publication of scientific reports from the 1970s on. This prediction was incorrect (Figure 6). In fact, there appears to have been a gradual decline in the incidence of "negative" reports such that only one more appeared after 1949 (the entry for the 1980s is anomalous as there was only one entry for this decade (Table 1)). The decline in the incidence of negative reports may be due to the disappearance of references to the species as an agricultural pest in more modern references, since this category made up the majority of "negative" references in the earlier European phase.

I also predicted a decline in newspaper articles expressing positive sentiment towards noisy miners in the period after scientific confirmation of their deleterious ecological impacts. There was, however, no clear response to support the prediction. Whilst "positive" articles peaked between 1910 and 1939 (Figure 6), they continued throughout the post-war period, declining from the 1970s onwards. In the absence of a clear trend, it is difficult to attribute this decline to a change in cultural attitude. There are a number of possible explanations for the lack of a clear trend. Popular culture may not have been aware of the effects of the noisy miner indicated by the scientific literature, or the scientific literature may not have dispelled positive feelings towards this native species. In some items in popular culture, for example, animosity towards the exotic Indian myna contrasted with more positive sentiment towards the native noisy miner (Spokesbird for the Order, 1995). A further explanation may be a time lag between the inception of new scientific knowledge and public understanding. Lags between research and policy, practice or industrial

⁶ The Australian magpie was chosen for comparison as it is consistently among the nation's favourite birds. It came second to the splendid fairy wren in a 2013 poll conducted by Birdlife Australia (Wilson, 2013)).



Figure 6. Proportion of newspaper articles containing positive, negative or neutral sentiments towards the noisy miner

Decade	Sample size
1840	1
1850	2
1860	10
1870	10
1880	10
1890	10
1900	10
1910	10
1920	10
1930	10
1940	10
1950	10
1960	4
1970	9
1980	1
1990	9

Table 1. Sample size of articles by decade forFigure 6

innovation are well known (Mansfield, 1998; National Research Council, 2008; Morris *et al.*, 2011). A further problem is that Trove provides archived newspaper articles only up to 1999. There were a number of articles in the media expressing negative sentiments towards the species after this period, and more in other media, such as internet sites, use of which became more common during this period as the role of print media declined. A final confounding factor is a decline in the incidence of newspaper reports about the noisy miner in the post-war period (Figure 2). A similar trend occurs for the Australian magpie (Figure 12, Appendix). It may be, therefore, that newspaper reports on native species generally declined over this period.

5.3.5 What can the cultural record tell us about the changing place of noisy miners in the socialecological landscape?

My semi-systematic review of newspaper articles failed to show a clear quantitative change in cultural attitudes to the noisy miner in the period since European invasion up to 1999. However, a qualitative consideration of reports about the species indicate that some of the positive sentiments expressed in the period up to the 1970s contrast strongly with the negative sentiments expressed since the 1970s. Further, the source of negativity towards the species appears to have changed, with modern reports more likely to express negative sentiment due to the species ecological impacts than historical concerns about its impact on horticultural crops.

Positive views of the species have not disappeared completely. A number of state volunteer wildlife rescue services and several privately-uploaded YouTube videos describe how to rear orphaned noisy miner chicks. Noisy miners are the subject of a children's storybook (Gardner, 2001), and the birds' insect-eating habits are appreciated by at least one website:

they can also be a helper in the garden. These guys love to eat the little bugs and insects that get up to no good in your veggie garden. (Backyard Buddies, 2018)

In the dominant discourse about the species in mainstream media and the ecological community, however, negative sentiments such as "hyperaggressive," "overabundant," "bullying" and "despotic" are now the norm (Table 2).

5.3.6 Does the cultural phase shift reflect an ecological phase shift?

The noisy miner was recognised as an aggressive species from the earliest period in Australia's European phase, as exemplified by the annotation on Watling's

1788	Arrival of First Fleet; Watling's painting of a "chattering bee-eater" with annotation "always at war with others of the feathered tribe."
1854	First reports in eastern newspapers list the soldierbird as an agricultural pest.
1863	"the greatest pest to the vine grower" (Maitland Mercury).
1878	Soldierbird listed as the natural enemy of timber pests (Sydney Mail); "gallant little birds" re. their attacks on snakes (Wagga Wagga Advertiser).
1909	Poet Henry Lawson writes "The Soldierbirds."
1911	"Soldier Bird Club" at a NSW school encourages pupils to feed noisy miners.
1915	"Morning Song of the Noisy Miner" published in <i>Emu</i> ; author claims " the carol of the magpie is eclipsed by the song of the Miner."
1918	Soldierbird listed as an unprotected bird under the New South Wales Animals Protection Act 1918
1953	"aggressive to smaller birds and not good mixers" (Gannon).
1976	"Indiscriminate interspecific aggression" (Dow)
1988	"forms itself into pugnacious colonies which take over and dominate territories the size of hobby farms" (Canberra Times)
1997	"noisy miners affect avian diversity and abundance by aggressive exclusion of small birds" (Grey et al).
2003	"hyperaggressive behaviour," "reverse keystone species" (Piper & Catterall).
2004	"Noisy Miners - the indigenous pestthe mafia of the bird world" (ABC).
2011	"Noisy bullies " (Birds in Backyards); "Noisy miners form gangs"; "the thug of the avian world" (Adelaide Advertiser).
2013	Noisy Miner working Group established; publishes "Avifaunal disarray due to a single despotic species" (Maron et al).
2014	"Aggressive exclusion of birds from potential woodland and forest habitat by over- abundant noisy miners" listed as Key Threatening Process under EPBC Act.
2015	"obnoxious little gangs" (No Award); "I hate those fuckin things" (reddit.com).
2016	"Native or not, it's time to cull noisy miners" (ABC); "Beating the bullies" (Loyn et al); "The birds we love to hate" (Australian Geographic).

Table 2. Changes in cultural perceptions of the noisy miner, 1788-2016

painting (1788-1792). References to the species' aggression towards other species appear consistently over the next two centuries. After the first ornithological journals were established in the early 20th Century, noisy miners featured in many articles (Zietz, 1914b; Anon, 1915; Anon, 1917; Hyem, 1936; Binns, 1953) but mention of effects on small woodland birds is conspicuously absent until 1953 (Gannon, 1953). Several reports indicate small birds nesting close to noisy miners, including one small woodland fragment in which three groups of noisy miners were nesting (Zietz, 1914a; Norton, 1922; Althofer, 1934; Bourke, 1949). Three nesting coteries in one fragment constitutes a colony by today's definitions.

There are two possible explanations for the absence before 1953 of reports indicating that noisy miner aggression affected small woodland birds. Either it was not happening, or it was

not noticed. It is possible that up to 1953 it was not yet happening on a scale that was apparent to *ad hoc* surveying. Early naturalists frequently recorded their observations in the minutest detail so it seems implausible that the phenomenon would not have been noticed had it been occurring at a large scale. My study has not yielded a definitive answer to which of these explanations is correct. Given the important role of vegetation configuration in determining noisy miner colonial behaviour, however, it is plausible that habitat modification in the early post-war period had not yet reached the necessary threshold for a generalized dominance of remnant woodland by noisy miners.

I hypothesise that before the ecological impacts of the accelerated post-war clearing took effect, at a landscape scale noisy miners in low densities existed alongside small woodland birds. At some point during the post-war period of accelerated clearing, a threshold of landscape change was crossed or a time lag expired. The level of habitat modification then interacted with the habitat preferences of noisy miners to create dominance of woodland fragments by noisy miners at a sub-continental scale. It is difficult to draw firm conclusions from discontinuous historical records of noisy miner behaviour, distribution and abundance. Nevertheless, the changes in cultural attitude towards the species in reports over the two centuries of the European phase seem to coincide with the known trajectory of habitat modification and with modern understanding of the species' habitat preferences.

5.3.7 Two centuries of clearing: towards a timeline for the transition from native to nemesis

In broad terms, the clearing of eastern Australia's woodlands occurred over two phases. The first was a relatively slow, government-supported development through the 19th and early 20th Centuries. The second was the "Great Acceleration" (Steffen *et al.*, 2015), a period of rapid growth of the agricultural industry initiated in the immediate post-war years and continuing into the late 1990s (Evans, 2016). The rise of the noisy miner and the consequent ecological impacts appear to loosely follow these two phases.

5.3.7.1 The first 150 years

The first phase of environmental transformation occurred as pastoralism moved outwards from the first coastal settlements. The merino was introduced nine years after the arrival of the First Fleet and by the 1850s there were about 18 million sheep in the country (Blainey, 1980). Whilst pastoralism did not require the broadscale clearing of woodland necessary for arable production, the presence of ungulates had impacts on soil structure and nutrient cycles (Muir, 2014). Inappropriately high stocking rates in response to the irregular years of good rain, combined with drought meant that grazing often

> consumed the capital and may have caused permanent changes meaning, in ecological terms, a phase shift (Hobbs and Hopkins, 1990, p93).

After the 1860s broadscale clearing accelerated as wheat production increased, assisted by the greater availability of labour following the gold rushes (Blainey, 1980). In the 20th Century, government-supported expansion of the area under cultivation continued and technological advancements increased productivity which in turn incentivized further clearing (Hobbs and Hopkins, 1990). In New South Wales, a state of 80.9 million ha, 25.7 million hectares of native vegetation were ringbarked and partially cleared between 1893 and 1921 (Glanznig, 1995).

In areas of woodland with a shrubby understorey, grazing would have permanently simplified the vegetation structure in the way that fire may have done cyclically in the pre-colonial era (M. Doherty, pers.comm.2017, ANU). This simplification in structure is likely to have made such areas more attractive to noisy miners. There is evidence of major changes in bird assemblages elsewhere in Australia as a result of pastoralism even before broadscale clearing occurred (Franklin, 1999). However, there are no records of an impact of noisy miner aggression on smaller woodland birds during this period. Records of the noisy miner as an agricultural pest suggest an abundant species but there is no indication of the domination of landscapes. This is consistent with a threshold effect or a lag phase before responses by the species to modified landscapes became apparent.

Historical reports of sightings of species can be used to build a picture of how a species spreads across the landscape (Abbott, 2002). Historical references to changes in distribution of noisy miners are limited but indicate changes in distribution from 1867 (see section *Changes in distribution and abundance* above). Miners are sedentary species and colonise landscapes slowly (Maron *et al.*, 2013). In common with many cooperatively-breeding passerines, high survival rates coexist with low reproductive output (Russell and Rowley, 1993; Clarke, 1995). It is likely, therefore, that changes in distribution and abundance occurred slowly in response to habitat modification.

5.3.7.2 The next 50 years: accelerated clearing and a new threatening process

Australia's post-war economic boom saw the biggest rise in broadscale clearing of native vegetation (Bedward *et al.*, 2007) (Figure 7). In the 45 years after 1945, as much native vegetation was cleared as in the previous 150 years (Glanznig, 1995). The pattern of land clearing in New South Wales meant that landscapes passed through a number of states from variegated to relictual (Bedward *et al.*, 2007; Fischer and Lindenmayer, 2007). This period of accelerated clearing was accompanied by the biggest ecological phase shifts in the sheep-wheat belt of eastern Australia (Hobbs and Hopkins, 1990; Yates and Hobbs, 2000; Muir, 2014) and by corresponding changes in bird assemblages (Reid, 1999). This period also marks the first report of a potential impact of noisy miner aggression on small woodland birds (Gannon, 1953).

Clearing for agriculture was faster and on a larger scale than the cyclical vegetative changes that had been occurring in Australia over climate cycles that spanned millennia. This rapid clearing limited the capacity for the existing biota to develop adaptive mechanisms. Eurasian agriculture, in contrast, developed over as much as 11000 years, meaning that some degree of ecological adaptation occurred in parallel with the developments of the human economy (Hobbs and Hopkins, 1990). The outcome in Eurasia now is ecosystems of much lower biodiversity than originally, but in a relatively stable state (Hobbs and Hopkins, 1990). Australia's agricultural development has occurred over just two centuries (or a much shorter period in later-colonized regions) so ecosystems are in their most sensitive stage with no natural resilience to the extreme disturbances imposed upon them. The result has



Figure 7. Area under cereal crops in New South Wales 1860-2000 Dashed line shows monotonic trend in area cleared for cropping (Source: Bedward et al 2007, reproduced with permission)

been a rapid phase shift to novel ecosystems (Hobbs *et al.*, 2006). Such ecological developments occur after an initial lag phase but agricultural development in Australia did not wait to see the impacts (Hobbs and Hopkins, 1990). As US forester, Overton Price noted,

It is the history of all great industries directed by private interests that the necessity for modification is not seen until the harm has been done and results have been felt (Price, 1903, p309).

Noisy miner aggression as threatening process must be seen within the context of the broad front of threatening processes that resulted from European settlement and expansion. Clearing of temperate eucalypt woodlands of eastern Australia has resulted in absolute losses of habitat along with fragmentation and degradation (Tulloch *et al.*, 2016). These processes are different from pre-European ecosystem processes and have had well-documented deleterious effects on ecosystems at all levels of biota (Hobbs and Hopkins 1990). The result has been local, regional and global extinctions (Yates and Hobbs 2000). The loss of up to 80% of southern temperate woodlands has seen proportional declines in small woodland birds (Connor and McCoy, 1979; Ford *et al.*, 2001; Woinarski *et al.*, 2006). Changes in

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resource availability have changed interspecific competition regimes and contributed to the changes in bird assemblages now seen across eastern Australia (Ford *et al.*, 2001; Watson, 2011).

Fragmentation of remnant woodlands has further impacted small birds through loss of connectivity (Saunders *et al.*, 1991; Ford *et al.*, 2001). Woodland and forest fragments, with high proportions of edge habitat, have fostered colonisation by noisy miners (Oldland *et al.*, 2009). Finally, degradation of remnant woodlands has occurred through changed hydrological, nutrient, grazing and fire regimes, and the entry of invasive weeds. The simpler vegetation structure that has resulted favours efficient defence by noisy miners through limiting possible refuges for smaller woodland birds (Maron *et al.*, 2013). One consequence of these multiple threatening processes has been the sub-continental dominance of remnant woodlands by the noisy miner (Mac Nally *et al.*, 2012; Maron *et al.*, 2013).

5.4 Conclusion: native to nemesis

Invasive species are exotic species introduced to a new environment where some advantage over native species, such as freedom from indigenous diseases or parasites, means that the invasive species can outcompete native species (Buckley and Catford, 2016). Overabundant species are native species whose abundance exceeds the cultural or ecological carrying capacity of an environment (Caughley, 1981; Garrott *et al.*, 1993; Dubois *et al.*, 2017). Although cultural distinctions are made between overabundant native species and exotic species (Low, 2007; Davis *et al.*, 2011), the process by which they exert their ecological impact is similar for the two groups. Overabundant species are, in effect, native species to which a new environment has been presented. In this new environment, frequently an anthropogenic novel ecosystem, the overabundant species has some competitive advantage over native competitors and therefore may become a threatening process to less advantaged competitors (Rothstein and Peer, 2005; Livezey, 2010).

Noisy miners have become the nemesis of small woodland birds due to the convergence of anthropogenic landscape transformation and the competitive behaviour of noisy miners. The historical record provides anecdotal evidence of changes in distribution and abundance. Whilst there is no evidence that the competitive behaviour of noisy miners has changed, there is evidence that the ecological effects of that competition have changed.

The decline of small woodland birds is the result of multiple threatening processes, aggressive exclusion by noisy miners being just one. Extensive deforestation in the sheep-wheat belt of eastern Australia since European settlement has seen proportional losses of biodiversity, particularly of many small woodland birds (Paton and O'Connor, 2009; Ford, 2011a). Increases in the abundance of noisy miners in recent decades further threaten some of these already-declining species and an extinction debt remains to be paid (Ford, 2011b). The novel ecosystems represented by the fragmented agricultural landscapes of inland eastern Australia are ideally suited to colonisation by noisy miners (Dow, 1977; Arnold, 2000; Montague-Drake *et al.*, 2011; Mac Nally *et al.*, 2012). The problem has been developing for two centuries, with the most noticeable impacts becoming apparent since the peak clearing periods of the second half of the 20th Century (Dow, 1977; Maron *et al.*, 2013). The noisy miner's sedentary habit and communal defence of remnant patches of eucalypt woodland have meant that natural interspecific aggression common to many honeyeaters has become a threatening process in the case of this one honeyeater.

More recently, the noisy miner population seems to have declined slightly in some areas though not sufficiently to show an immediate reduction in their ecosystem impacts (Lindenmayer *et al.*, 2018b). It may be that they are reaching the limits of their range and abundance in affected areas. Climate change and continued clearing of native vegetation in agricultural landscapes, however, may permit further expansion of the species' range and abundance (Mac Nally *et al.*, 2009; Mac Nally *et al.*, 2014).

Novel ecosystems present novel challenges for management to maximise their ecological value, particularly in the economically productive landscapes favoured by the noisy miner (Fischer *et al.*, 2006; Lindenmayer *et al.*, 2008). In productive landscapes such as the sheep-wheat belt of eastern Australia, where most remnant native vegetation is on private farms, the traditional model for addressing threats through a network of comprehensive, adequate and representative reserves is ineffective. To deal with the numerous threats that permeate the landscape and are often unaffected by protected area boundaries, a whole-of-landscape approach to conservation is necessary, taking into account actions both on and off reserves (Margules and Pressey, 2000; Fischer *et al.*, 2006; Fischer *et al.*, 2014).

Historical experimental culling of noisy miners appeared to offer some possibility of controlling abundance of the species (Grey *et al.*, 1997; Grey *et al.*, 1998). However, more recent culls in highly-modified agricultural landscapes have been shown to be ineffective due to rapid recolonisation (Davitt *et al.*, 2018; Beggs *et al.*, 2019). Recognising the key role of social-ecological change in the historical genesis of the noisy miner problem may offer an approach to managing the ecological impacts of noisy miners. Environmental history is therefore a suitable

medium through which to frame appropriate strategic responses. Notwithstanding possible hysteretic effects (Mac Nally, 2008; Suding and Hobbs, 2009), landscape restoration may offer benefits to small woodland birds directly by providing habitat, and indirectly by reducing noisy miner abundance (Hastings and Beattie, 2006; Lindenmayer *et al.*, 2010; Grey *et al.*, 2011; Lindenmayer *et al.*, 2012; Ikin *et al.*, 2018; Lindenmayer *et al.*, 2018a).

Every generation reinterprets history through the prism of contemporary values. The historian's work is

> a continuous process of interaction between the historian and his facts, an unending dialogue between the past and the present (Carr, 1961, p35).

This is perhaps nowhere truer than in environmental history given that policies and values about the environment have changed markedly over the course of the European phase of Australian history. The productive values seen in the landscape by settlers were clearly different from the conservation values considered by modern ecologists. Initially, no amount of destruction of native biodiversity seemed to impact the productive value of the land sufficiently to encourage a change in policies or values (Muir, 2014). Now, threats to provision of ecosystem services are recognized, at least by the scientific community (Costanza *et al.*, 1997; Díaz *et al.*, 2018; Diaz *et al.*, 2019). Some sectors of the population recognise intrinsic value in the planet's ecosystems and the other species with which we share the planet (Bruskotter *et al.*, 2015; Vucetich *et al.*, 2015). Acknowledging environmental history as we move into the Anthropocene may offer an antidote to the environmental amnesia that allows us to continue to ignore our impacts:

> Rather than float in an unconnected present, environmental history can provide some context and story as to how we got here (Dovers, 2000, p21).

If we fail to consider the trajectory that has led us to where we are, we are doomed to become living proof of the clichéd paradox that we learn from history that we learn nothing from history.

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Appendix

Colonial period paintings and habitat potentially suitable for noisy miner colonisation

This small selection of paintings shows some examples of open grassy woodland, or "parkland," as well as edge habitat in forest patches. Such fragmentation could have come about as a result of indigenous fire regimes. Such habitat conforms, in outward appearance at least, with the kind of vegetation structure that today would be colonised by noisy miners.



Figure 8. Joseph Lycett, 1821, view from Constitution Hill, Tasmania



Figure 9. Martha Berkeley, c1840, Mt Lofty, South Australia



Figure 10. Robert Hoddle, 1847, Victoria (Mt Macedon?)



Figure 11. Eugene von Guerard, 1858, Mt Eccles, Victoria

Classification of results of Trove search, all categories

Article (3,682) Book chapter (7) Conference paper (4) Journal or magazine article (323) Other article (68) Report (17) Review (2) Book (45) Braille (2) Illustrated (32) Large print (1) Photograph (41) Thesis (24) Sound (19) Interview, lecture, talk (2) Other sound (16) Recorded music (1) Art work (9) Data set (6) Printed music (4) Microform (3) Archived website (2) Audio book (2) List (1) Periodical (1) Journal, magazine, other (1) Poster, chart, other (1) Published (1) Unpublished (1)

Total (3842)

Search term

"noisy miner"~0 OR "soldier bird"~0 OR "mick* miner"~0 OR "snake bird"~0 NOT rac* NOT "snakes, birds"

Search term glossary

Term	Meaning
"noisy miner"~0	The terms in inverted commas must be immediately adjacent to each other ie the number of words separating them = 0.This avoids picking up phrases such as "a noisy group of miners assembled outside Kalgoorlie Town Hall"
"mick* miner"	Any word beginning with "mick" will be included in the search. This was to account for the different possible spellings, mickey and mickie
NOT "snakes, birds"	This excluded phrases that contained lists such as "snakes, birds"
"soldier bird" , "snake bird"	Composite names soldierbird and snakebird appeared sometimes as one word and sometimes hyphenated. Leaving a space between the two terms accounted for both forms



Figure12. No. of newspaper articles about magpies, 1840 – 1999 (Search term: "magpie" NOT foot* NOT rac*)



Figure 13. Trove search results for references to the noisy miner in journals, articles and data sets