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

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Abstract. Overabundant native animals cause a variety of human–wildlife conflicts that 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 km^2). 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 12 months after a culling program and found that immediate recolonization from the surrounding landscape negated the impact of the cull. We hypothesize 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. Modeled 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 three to five 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.

Key words: compensatory immigration; cull; ecological release; ecosystem recovery; evidence-based environmental management; interspecific competition; Manorina melanocephala; *overabundant native species; population control; threat management.*

Introduction

Changes in distribution and abundance of native animals in response to anthropogenic habitat modification and other threatening processes are not uniform. While 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 coexisting species and the disturbance of ecological

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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 hybridization (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 modeling 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 is 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 modeling 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, only 10 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 hybridization, 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 recognized 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 subcontinental 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). Localized culling and translocation have been used to manage populations of two other Manorina species, the Bell Miner (*Manorina melanophrys*; Clarke and Schedvin 1999) and the Yellow-throated Miner (*Manorina 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 12–16 months following removal were achieved (Grey et al. 1997, 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 0.6–0.8 birds/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, 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 five 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 (Appendix S1: Fig. 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 than sites where less effort was expended. Because we aimed to reduce 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.

Methods

Study region

The study was conducted from 2015 to 2017 in a total of 208 ha of remnant woodland patches over a landscape of 471 km^2 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 southeastern Australia (Fig. 1). This region has a continental climate with hot dry summers and cold winters, with average annual rainfall 624 mm (Gundagai) and 526 mm (Junee) (Bureau of Meteorology 2018).[7] 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% 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

[7] http://www.bom.gov.au/climate/data/

(*Eucalyptus macrocarpa*), yellow box (*Eucalyptus melliodora*), Blakely's red gum (*Eucalyptus blakelyi*), and some mugga ironbark (*Eucalyptus 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).

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 4 to 49 ha (mean = 13 ha). 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 1,142 m apart (mean = 2,224 m, maximum = 6,405 m) to ensure spatial independence and discourage recolonization following the cull. This was based on Dow's (1979) indication

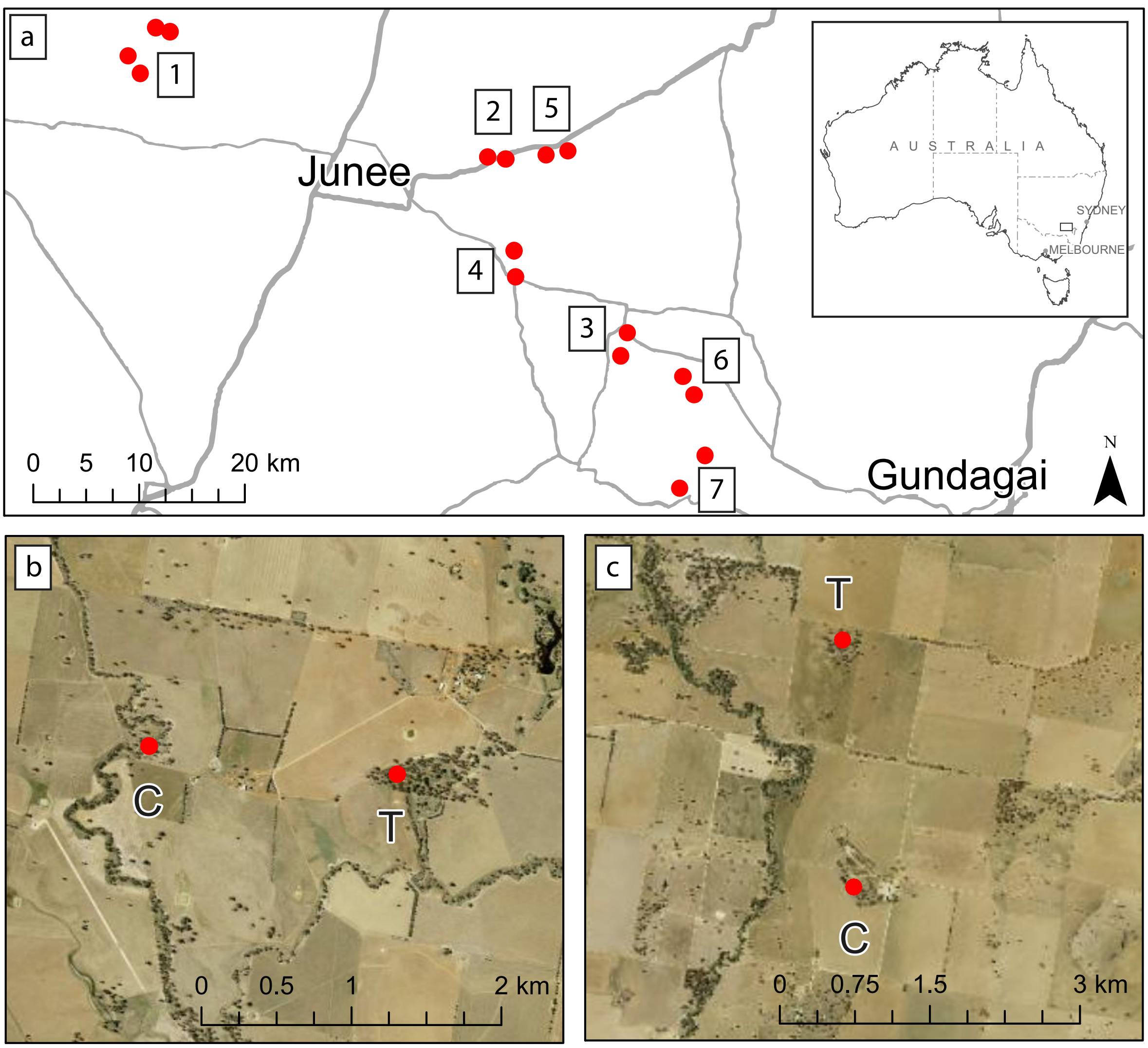

Fig. 1. (a) Study region in southeastern Australia. Numbers in boxes refer to the seven farms on which treatment and control patches were located. (b, c) Maps showing the relationship of treatment and control patches, and landscape configuration, on two example farms. Panel b is Farm 2; panel c is Farm 4 (base maps: copyright Spatial Services, the State of New South Wales, Australia).

of a maximum Noisy Miner home range of about 212 m. Based on our belief that a coherent social connection between coteries of Noisy Miners could not be maintained across hundreds of meters 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).

Experimental treatment

We culled Noisy Miners from the eight treatment patches during the non-breeding 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 500 m 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-min 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.

Survey protocols

To ensure standardized experimental monitoring units, we surveyed a randomly located 2-ha study site based around a marked 200-m 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 12 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 15-minute walking count of Noisy Miners up to 50 m either side of the 200-m 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 that 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-yr period.

Statistical analysis

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

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 generalized 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. 2013). Akaike information criterion (AIC) scores were lower when we used a negative binomial distribution, indicating overdispersion of data. We modeled 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 recolonization. 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. (1) Patch area: we expected larger patches to support larger populations of Noisy Miners in the 2-ha experimental unit due to larger resource concentrations in these patches (Connor et al. 2000). (2) Productivity: Noisy Miners favor productive sites, so we used Topographic Wetness Index, sensu Montague-Drake et al. (2011) as a proxy for productivity. (3) Tree stem density: we used the average of the number of tree stems counted in a 20 × 20 m quadrat at each of the three marker posts along the 200-m 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 stems/ha (Maron 2007). All the sites in this study were open eucalypt woodland with low density of tree stems (5.1 ± 4.0 stems/ha; mean ± SD), but based on previous studies, we assumed that sites with lower stem density would have higher Noisy Miner abundance (Howes et al. 2010). (4) Percent tree cover within 100 and 1,000 ha 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).

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, *personal communication*).

Does greater culling effort result in a greater reduction in Noisy Miner abundance?

We combined results from the first and second questions in a ROI 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.

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 ± 3.9 birds/ha (mean ± SD). We achieved a clean kill rate of 86%. The maximum number of birds culled in a patch was 131 (patch size = 19.9 ha) and the minimum was 36 (patch size = 16.9 ha). Noisy Miner abundance was highly variable in time and space and was greater during the winter non-breeding season than the summer breeding season (Fig. 2). Mean abundance per 2-ha site was lowest in post-cull treatment sites (5.8 ± 5.3), and highest in post-cull control sites (7.1 ± 5.9).

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; Appendix S1: 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 d after the second cull), modeled post-cull changes in Noisy Miner abundance

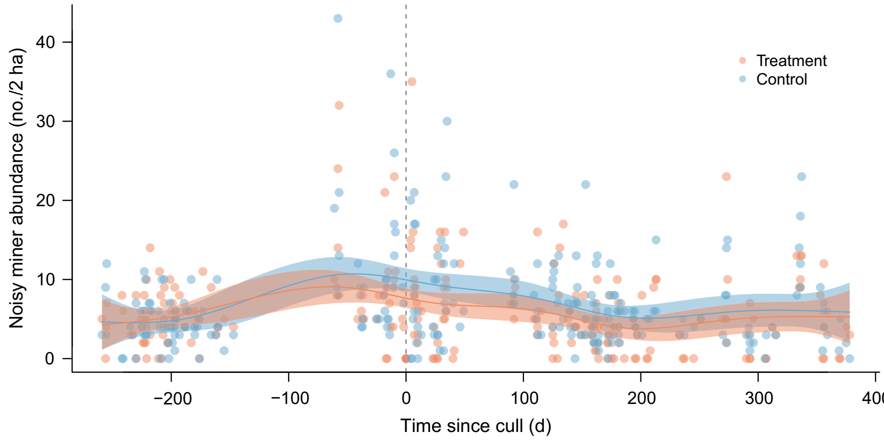

Fig. 2. Plot of Noisy Miner abundance over the period of the study. Each point represents one site survey. The fitted curves show the trajectory, with 95% confidence intervals, of Noisy Miner abundance. The vertical line indicates the time of the final cull (May–June 2016). The red point at zero abundance 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.

(with 95% confidence intervals) were 4% (−12%, 23%) for control sites and −22% (−35%, −8%) for treatment sites (Fig. 3a). When we compared pre- and post-cull breeding seasons (up to 251 d post-cull), 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 d 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%).

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 (Fig. 3b). 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 (Fig. 3b, rightmost plot). A full list of models with AIC scores is provided in the Appendix S1: Table S2.

Table 1. Model parameters used in final model as predictors of Noisy Miner abundance (entire 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.

Effects	Coefficient estimate†	Confidence interval Lower	Confidence interval Upper
Fixed			
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, variance (log scale)			
Farm	0.01		
Site	0.14		

†Back-transformed.

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$13,069, labor accounting for 91% of this (Table 2). This is an average of AU$24 per bird (± AU $6) or AU$136 per ha of patch cleared (±AU$17). All Noisy Miners using treatment sites at the time of the cull were removed. The average number of birds removed per person-hour of culling effort was 2.9 (range 1.5–4.3). More birds were culled in larger sites (eight treatment sites, df = 6, $r = 0.60$, $P = 0.12$). Effort and patch area 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: Fig. S2, for details of relationship between effort, patch area, and number of birds culled.)

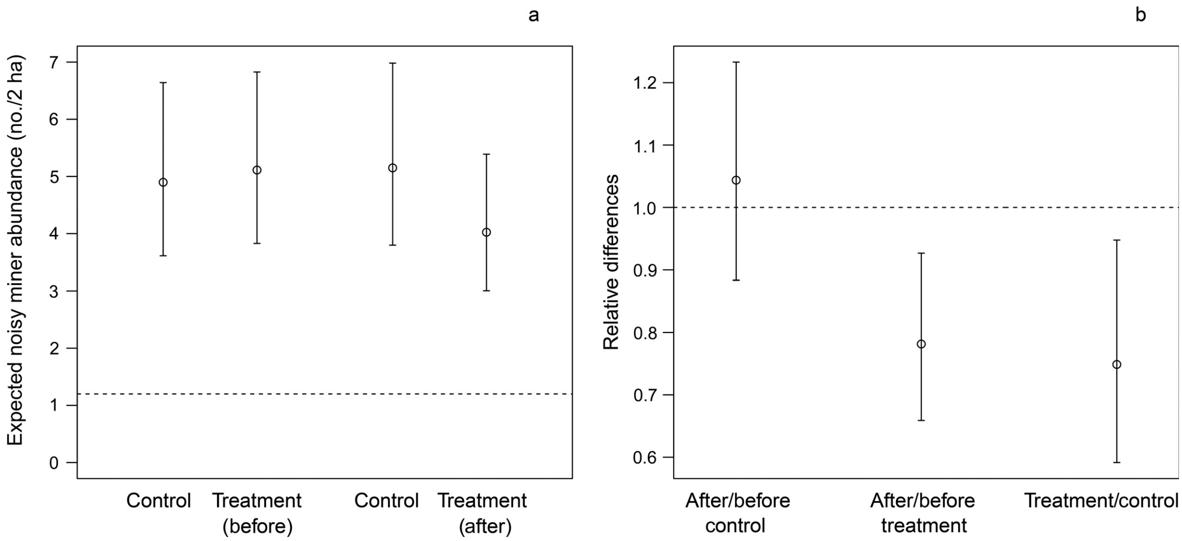

FIG. 3. (a) Expected Noisy Miner abundances over full period of study according to the best model, with 95% confidence intervals. The dotted line at 1.2 birds/2 ha is the impact threshold of Noisy Miner abundance on species assemblages (Thomson et al. 2015). (b) Relative differences in expected Noisy 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.

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 (Appendix S1: Fig. 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 (Appendix S1: Table S3). Confidence intervals for the effort × phase coefficient estimates for all time periods modeled overlap zero.

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 scale and a landscape scale, we related management effort to the change in abundance of the species and assessed ROI. 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 subcontinental 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 (Fig. 2) and that

TABLE 2. Total costs of the Noisy Miner cull partitioned into labor costs, travel costs, and perishables (ammunition).

Expense	AU$
Labor (cull), 212 person-hours at AU$50 per hour	9,700
Labor (travel), 43 person-hours at AU$50 per hour	2,150
Labor (total)	11,850
Travel (980 km at AU$0.75/km)	735
Ammunition (approximately 1,100 rounds at AU$220 per 500)	484
Total cost	13,069

Note: Costs are given in Australian dollars.

post-cull 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.

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 three to five times higher than published impact thresholds (Fig. 3a; 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, *personal communication*), and prior experimental results (Grey et al. 1997, 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. (1) 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. (2) Birds have moved in from an adjacent colony or colonies. Explanation 2 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 1978) 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 (Fig. 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 recolonize 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, 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 localized culls difficult. There is an urgent need, therefore, to synthesize 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 recolonization. Patches might then remain free of Noisy Miners long enough for small woodland birds to move back in. Short of a landscape-scale 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 recolonization from further afield since farms have porous boundaries.

The fundamental unknown here is what promotes Noisy Miners to leave their home range and recolonize another site following a cull. One suggestion has been to cull only the inner core of a colony (M. Maron, *personal communication*) 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).

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$2,800 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 1 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 three 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 birds/ha on occasions, Fig. 2), this would mean a minimum of 30 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 20-ha project over 10 years have been estimated at AU$2,580/ha (Ansell et al. 2016). While this is almost 18 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).

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 ROI, particularly given that Noisy Miner abundance remained above ecological impact thresholds (Appendix S1: Fig. S3, Table S3).

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 preempt 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 the following. (1) 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. (2) 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. (3) 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. (4) 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 (Beggs et al., unpublished data) and a small decline in artificial nest predation rates (Beggs et al. 2019). (5) 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. Finally, (6) other management actions that might, instead of or as well as a cull, achieve better outcomes (Tulloch et al. 2016).

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 recolonization 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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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1846/full