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Conservation problem

Declining small woodland birds in a fragmented agricultural landscape

Nest predation principal cause of breeding failure for many small woodland birds


Known nest predator, Noisy miner

Experimental intervention + monitoring

Removal of overabundant nest predatory bird, the noisy miner *(Manorina melanocaphala)*

Artificial nest predation rate as proxy for breeding potential of small woodland birds


Identified nest predator ii, Australian magpie

Outcomes

Noisy miner abundance 28% lower in treatment than control (Fig S6)

Noisy miners responsible for 18.3% of total nest predation (Fig S3)

Non-significant (negative) change in artificial nest predation in treatment vs. control (Fig 3)

Five other nest predatory birds identified (Fig S3)

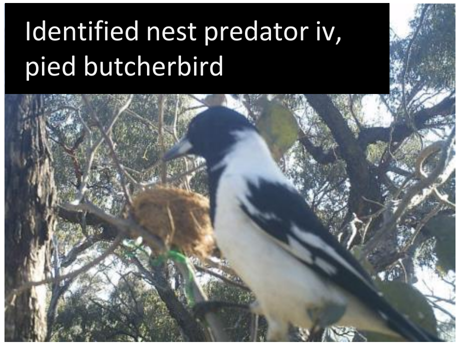

Identified nest predator iii, white-winged chough

Hypothetical Mechanism


Identified nest predator v, Australian raven

No significant change suggests compensatory nest predation

Direction of change suggests additive nest predation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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

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.[5] 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

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

or invasive animal (Doherty et al., 2015, Treves and Naughton-Treves, 2005). 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 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 alter species assemblages (Johnson et al 2011). Small woodland birds are in particular decline (Ford, 2011). 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 (Lumpkin et al., 2012, Ibáñez-Álamo et al., 2015).

One aggressive species associated with nest predation and breeding failure of vulnerable species, is the noisy miner (*Manorina melanocephala*), a colonial honeyeater. Since European settlement, the noisy miner has become overabundant at a sub-continental 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 (Maron et al., 2013, Mac Nally et al., 2012). Whilst there is evidence of noisy miners predating artificial nests (Ross?), the principal impact of noisy miners on breeding success of small birds is through aggressively prevneting nesting attempts and nest destruction (Low, 2014). Small woodland birds 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)). Aggressive exclusion by 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 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 (Debus, 2006, Gardner and Heinsohn, 2007, Zanette, 2000). Culling of nest predators is an attractive management tool to reduce their impacts, but numerous other 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).

In a correlative study of the effect of noisy miner density on artificial nest predation rates, Robertson et al., (2014) found that the presence of noisy miner colonies invalidated the additive predation model. They attributed this finding to the keystone role of noisy miners in structuring species assemblages. Additive nest predation impacts breeding success of prey species because 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).

We present empirical evidence of the effects of culling noisy miners on artificial nest predation rates. We completed a controlled and replicated experimental cull of noisy miners in remnant woodland patches (Beggs et al., 2019) (accepted for publication). 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 are used widely as a means of identifying 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 noisy miner colonies (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 nest predation. Combined with camera monitoring, artificial nest predation experiments therefore provide essential information about the breeding potential of small birds in landscapes dominated by aggressive nest–predatory species.

We aimed to answer three 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?

Qu.3. Does a cull of noisy miners result in compensatory anest predation by other nest predators?

Based on the hypothesis that the additive predation model is invalid in areas dominated by noisy miners (Robertson et al., 2014), our *a priori* expectation was that the noisy miner cull would not impact artificial nest predation rates. We anticipated that other avian species of nest predators would 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 recolonisation (Beggs et al., 2019) (accepted for publication). 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 aggressive and nest predatory behaviour of recolonizing birds. 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). We therefore made no predictions about the outcome of the cull on nest predation rates nor on the likelihood of compensatory predation by recolonizing noisy miners or other species. 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.

Methods

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 nested 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).

BACI Study design

We conducted artificial nest predation experiments 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°03'55.5"S 148°06'18.7"E) and Junee (34°52'11.7"S, 147°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 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 (1977) indication of a noisy miner home range of about 200m. Noisy miners were present in all patches with consistent detection rates in monitoring since 2002 of more than 20% (Mortelliti et al., 2016).

Woodland birds are impacted by changes at site and landscape scales (Cunningham et al., 2014, Montague-Drake et al., 2011). 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.

Experimental treatment

We conducted culls during the non-breeding season in May and June 2016 using a 12-gauge shotgun and number 9 shot. 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)(accepted for publication).

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. whicker 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 we 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), nests and eggs were sprinkled with 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, 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.

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 the 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.

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):

$$\mathrm{CPA} = \frac{\mathrm{Perimeter}}{\sqrt{\mathrm{Area} \text{ x } 4\pi}}$$

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

Statistical analysis

Qu.1. Does a cull of noisy miners change the rate of artificial nest predation?
In this part of the analysis, we tested the hypothesis of Robertson et al., (2014) that the presence of noisy miner colonies negates the additive predation model. This hypothesis would be supported if overall nest predation rates remained the same even after a reduction in density of the noisy miner, implying operation of a compensatory predation model.

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). It was clear from summary statistics that the two nest types responded differently in the two phases of the experiment (Figure 2). We therefore included a Nest type:Phase interaction in our global model. 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.

Using the *R* package *MuMIn* (Barton, 2018), we assessed 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.

Model interpretation

A Treatment:Phase interaction would indicate 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 did an inverse logit transformation to convert odds in model output to probability.

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.

Qu.3. Does a cull of noisy miners result in compensatory nest predation by other nest predators?
In this part of the experiment, we further tested the Robertson et al., (2014) hypothesis that the presence of noisy miner colonies negates the additive nest predation model. If this is the case, we would expect to see compensatory nest predation by other species, or a greater level of predation by remaining or recolonizing noisy miners, in treatment sites after the cull. 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 construct a binomial model. Zero predation by noisy miners was recorded in control sites in Phase 0, 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 see 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.

Results

We found no evidence of a change in artificial nest predation rates as a result of the cull (Figure 3). 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 2). 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 only four cases of a mammal investigating or predating nests.

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(a)). We chose the most parsimonious of these as our best model. This model contained the base BACI variables plus Foliage cover, Nest type, CPA, Replicate and Phase:Nest type interaction. According to this model, the cull resulted in mean artificial nest predation in treatment sites 0.73 (0.33, 1.61) times the mean artificial nest predation in control sites (Figure 3 (b)). When we removed the Treatment:Phase term from the best model, the AIC score declined by 1.4. 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).

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 in Phase 0 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.

Qu.3. Does a cull of noisy miners result in compensatory nest predation by other nest predators?

In treatment sites, artificial nest predation by noisy miners, as a proportion of total predation where a predator was identified, increased from 27.8% in Phase 0 to 33.3% in Phase 1. In control sites, noisy miner predation increased from 0% in Phase 0 to 10% in Phase 1 (Table 3).

Our binomial model of predator identity (noisy miner/other) using 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).

Discussion

We set out to test empirically 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 and nest predatory bird have the potential to improve breeding outcomes for declining small birds and to investigate whether an additive or compensatory nest predation model operates in these ecosystems. We found no evidence of a change in post-cull nest predation between treatment and control sites in spite of a reduction in noisy miner density in treatment sites compared to control sites by a factor of 0.72 (0.54, 0.95) (Figure S6). We found that noisy miners accounted for 18.3% of total nest predation events where a predator was identified, but we failed to find conclusive evidence for either a compensatory or additive nest predation model. In the remainder of this paper, we consider research questions two and three further and suggest how our findings might inform management options to improve breeding potential of small woodland birds.

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

Noisy miners accounted 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. In cases such as this where the combined impact of other nest predators exceeds that of the species singled out for culling, culling is anyway less likely to have benefits for breeding success of target species (Fulton, 2018). Even if noisy miners were eradicated from treatment sites, the theoretical maximum reduction in nest predation would only be around a fifth. Given that breeding failure of small woodland birds can be as high as 90%, with nest predation the principal cause (Belder et al., (in press)), this may be insufficient to ensure population growth.

Qu.3. Does a cull of noisy miners result in compensatory nest predation by other nest predators?

The lack of a significant reduction in nest predation following the cull suggests, *prima facie*, that recolonizing noisy miners and/or existing other predators compensated for the predation foregone by culled birds. This appears to confirm the proposal by Robertson et al., (2014) that the additive predation model does not hold in the presence of noisy miners. However, the direction of the treatment effect (Figure 3(b)) is suggestive of additive predation: post-cull artificial nest predation in treatment sites was lower by a factor of 0.73 (0.34, 1.61) than in control sites. Error here is very large, which may be due to the limited statistical power inherent in our small sample size (eight treatment/control site replicates).

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 in both regards ((Doherty and Ritchie, 2017). Our experimental cull was no exception. Despite significant culling effort and expense (Beggs et al., 2019) (accepted for publication)., 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, Maron et al., 2013) due to recolonisation. We also saw no evidence of a reduction in artificial nest predation rates.

Interspecific and intraspecific social disruption and the potential for perverse outcomes

The role of noisy miners in nest predation is complicated, however, 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 a refutation of the additive 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, in a process analogous to mesopredator release, the potential exists for higher levels of nest predation following removal of noisy miners due to what we term “social release,” whereby noisy miners no longer exert social control over other nest predators. This effect could be mediated by a change in behavior or abundance of other nest predators, although in our study we found no relationship between the culling treatment and density of other nest predators.

We twice removed all noisy miners in treatment sites and twice those sites were recolonized by new birds (Beggs et al., 2019) (accepted for publication). We expected that this would change the intraspecific relations within recolonizing populations. Since the principal influence of the noisy miner on other species is its aggressive cooperative defense of colonized territory (Dow, 1977), we expected that the intraspecific social disruption caused by the cull might change the impacts of noisy miners on other species, at least in the short term. This 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 across taxa (Bodey et al., 2011, MacFarlane, 2014, McKinney, 2001).

Limitations of the study

Clear outcomes for the study 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), (D Belder, 2018, personal communication). 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. Another possible explanation for our inconclusive results is that noisy miners were not controlled sufficiently to allow for a clear compensatory response by other species.

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 (D Belder, 2018, personal communication). In another study, noisy miners accounted for only two out of 23 identified artificial nest predation events (R Crates, 2018, personal communication). Noisy miners have been observed destroying nests of the critically endangered Regent honeyeater (*Anthochaera phyrgia*). 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 cowbird species 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 this study, we failed to answer this question conclusively and 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.

At the landscape and patch scale, vegetative 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 (Davitt et al., 2018; Beggs et al., 2019 (accepted for publication)), 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. 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, and means that efforts to improve ecosystem function through vegetation restoration may ensure a more effective and long term benefit for declining small woodland birds.

Some idea of the likelihood of achieving fundamental objectives is necessary before seeking to apply more broadly expensive means objectives, such as culling programs. 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. This is likely to be particularly significant in times of resource scarcity such as drought. Any management attempt to reverse the decline of vulnerable species in the longer term, however, 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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Tables

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, 200**
			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 (*Rattus rattus & R norvegicus*) 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	**(XXXXXX et al., 2018, 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 for target species or other taxa	Unexpected increase in abundance of overabundant or invasive species	Increased juvenile survival or compensatory immigration; predator release; mesopredator release	**Increased abundance of an exotic herbivore when native apex predator removed**	**(Corbett, 1995)**
			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)

Table 2. Explanatory variables used in GLMMs

Predictor	**Expected impact on artificial nest predation rate**	**Variable type**	**Values**
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 Kleindorfer, 2009)	Categorical	1,2,3 (1 indicates 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 are nests there for predation, or that the eggs are artificial and therefore not worth predating.	Categorical	1,2,3 (1 is the first replicate)
Patch-scale features			
Total stems (Average no. of tree stems in a 20m x 20m quadrat at each of the three marker posts along the 200m site transect in each patch)	Noisy miners favour sites with lower stem density (Howes et al., 2010). We therefore expected sites with higher stem density to have lower nest predation rates.	Continuous	1 – 15.7 Mean = 5.1 SD = 4.0
Patch area	Patch area influences noisy miner density (Lindenmayer et al., 2018a, Maron et al., 2013)	Continuous	3.3 – 48.5ha Mean = 13.0ha SD = 10.9
Corrected perimeter to area ratio (CPA)	Patches with a higher CPA have relatively more edge so are likely to have more nest predation (Ibáñez-Álamo et al., 2015)	Continuous	112.9 - 397.0 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 al., 2011).	Continuous	0.04 – 23.5% Mean = 3.8% SD = 6.7%
Topographic wetness index (TWI)	TWI has been used as measure of productivity and has been shown to influence noisy miner density (Montague-Drake et al., 2011). Other than in models which	Continuous	-1.2 – 3.0 Mean = 1.1 SD = 1.2

	included noisy miner density, we included TWI as we considered it might be associated with 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 predation (Oppel et al., 2014).	Continuous	0 - 15/2ha Mean = 4.5/2ha SD = 3.1/2ha
Density of other known nest predators		Continuous	0 - 12/2ha Mean = 3.6/2ha

Table 3. Nest predator identity by Treatment and Phase

Phase	**Predator**	**Control**	**Treatment**
Phase 0	Noisy miner	0	5
	Other	11	12
Phase 1	Noisy miner	2	4
	Other	18	8

Figures

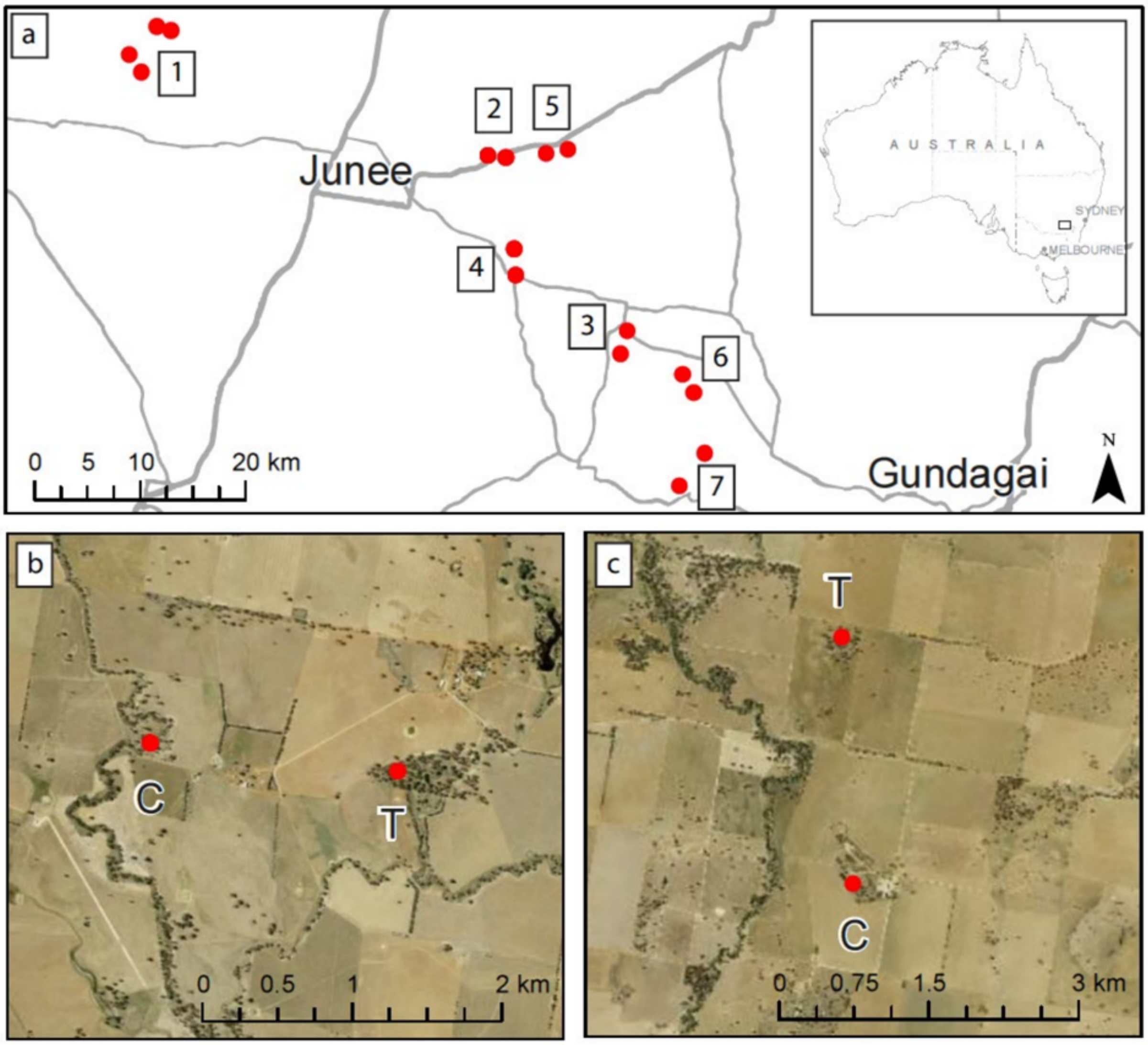

Figure 1. Study region in south-eastern Australia. a) Paired treatment/control study patches on seven farms. Numbers in boxes refer to farm number. b), c) Maps showing relationship of treatment and control patches, and landscape configuration, on two representative farms. b) is Farm 2; c) is Farm 4. (Base maps for b) and c): copyright Spatial Services, the State of New South Wales, Australia)

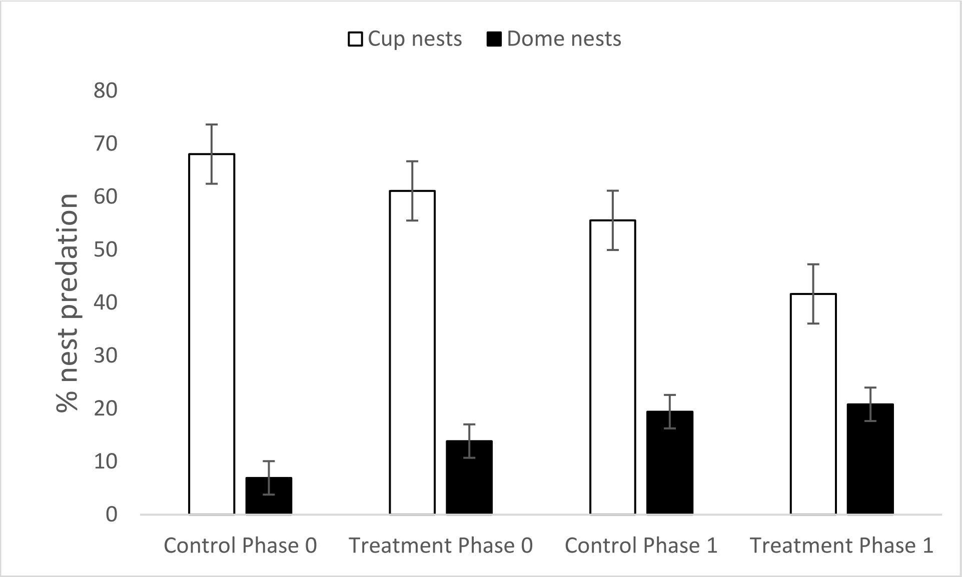

Figure 2. BACI predation rates of cup and dome nests, with standard error

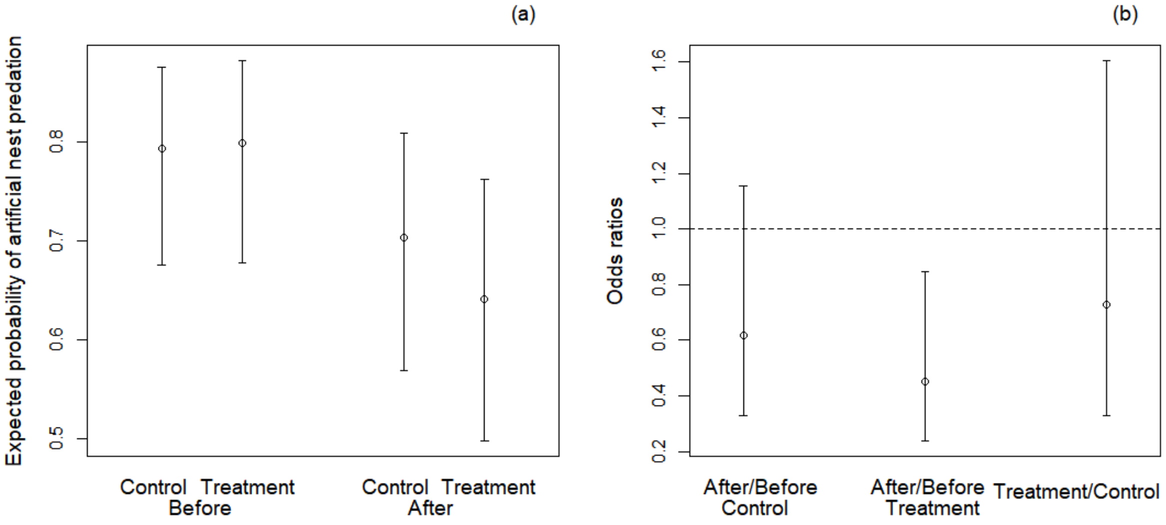

Figure 3. (a) Expected probability of artificial nest predation according to the best model, with 95% confidence intervals; (b) Odds ratios of artificial nest predation before and after the cull in treatment and control sites respectively, with 95% confidence intervals. The dotted line at 1.0 represents 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.

SUPPORTING INFORMATION

Figure S4. Typical study site, showing widely dispersed trees and lack of understory (source: Corresponding author)

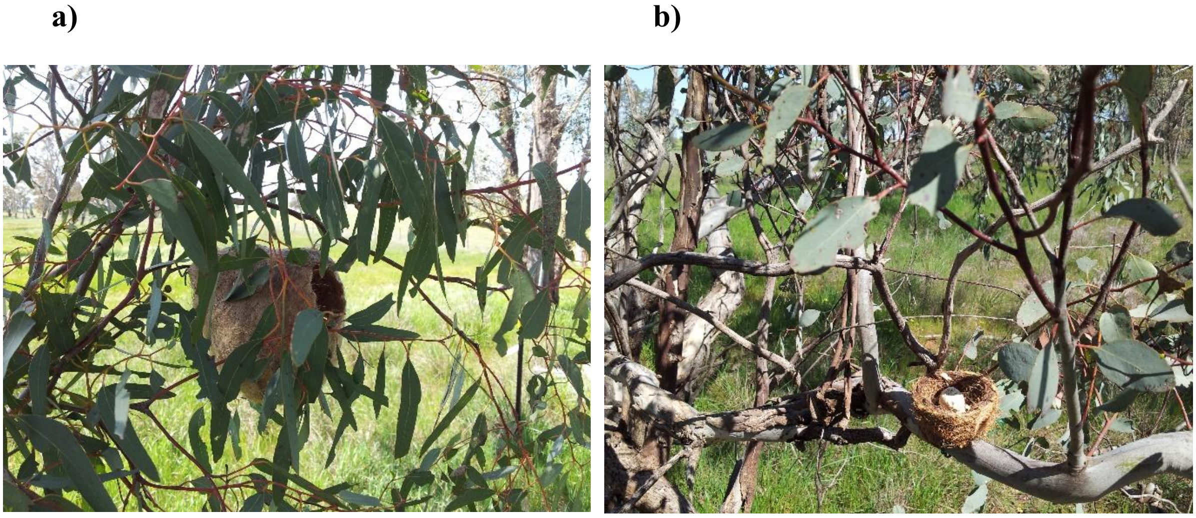
a)
b)

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

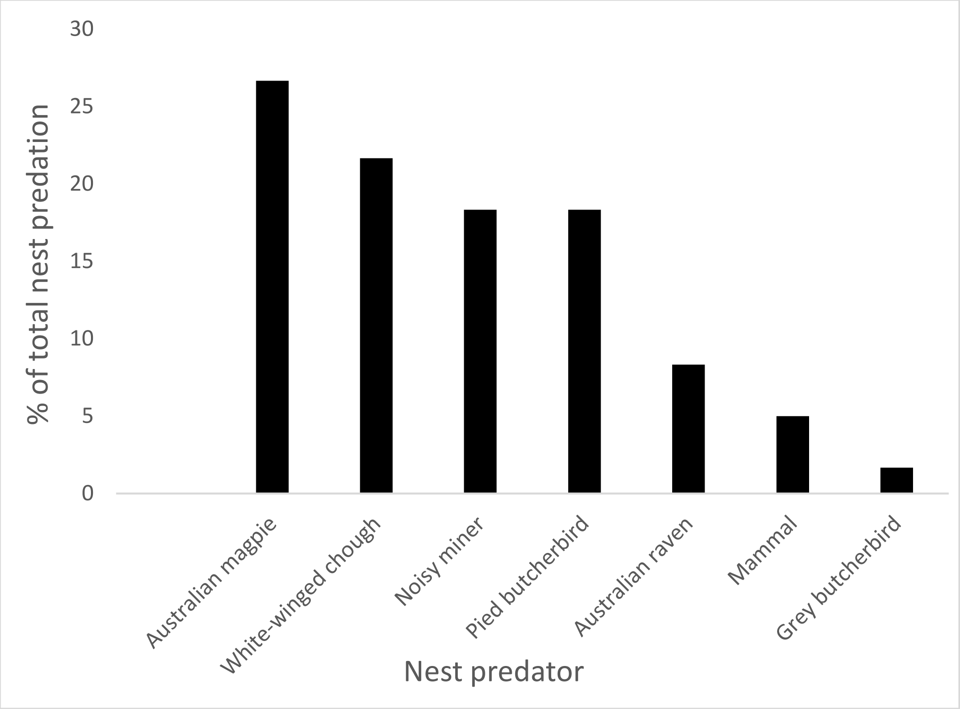

Figure S3. Contribution of nest predators to total nest predation over the whole study (Treatment and Control sites combined)

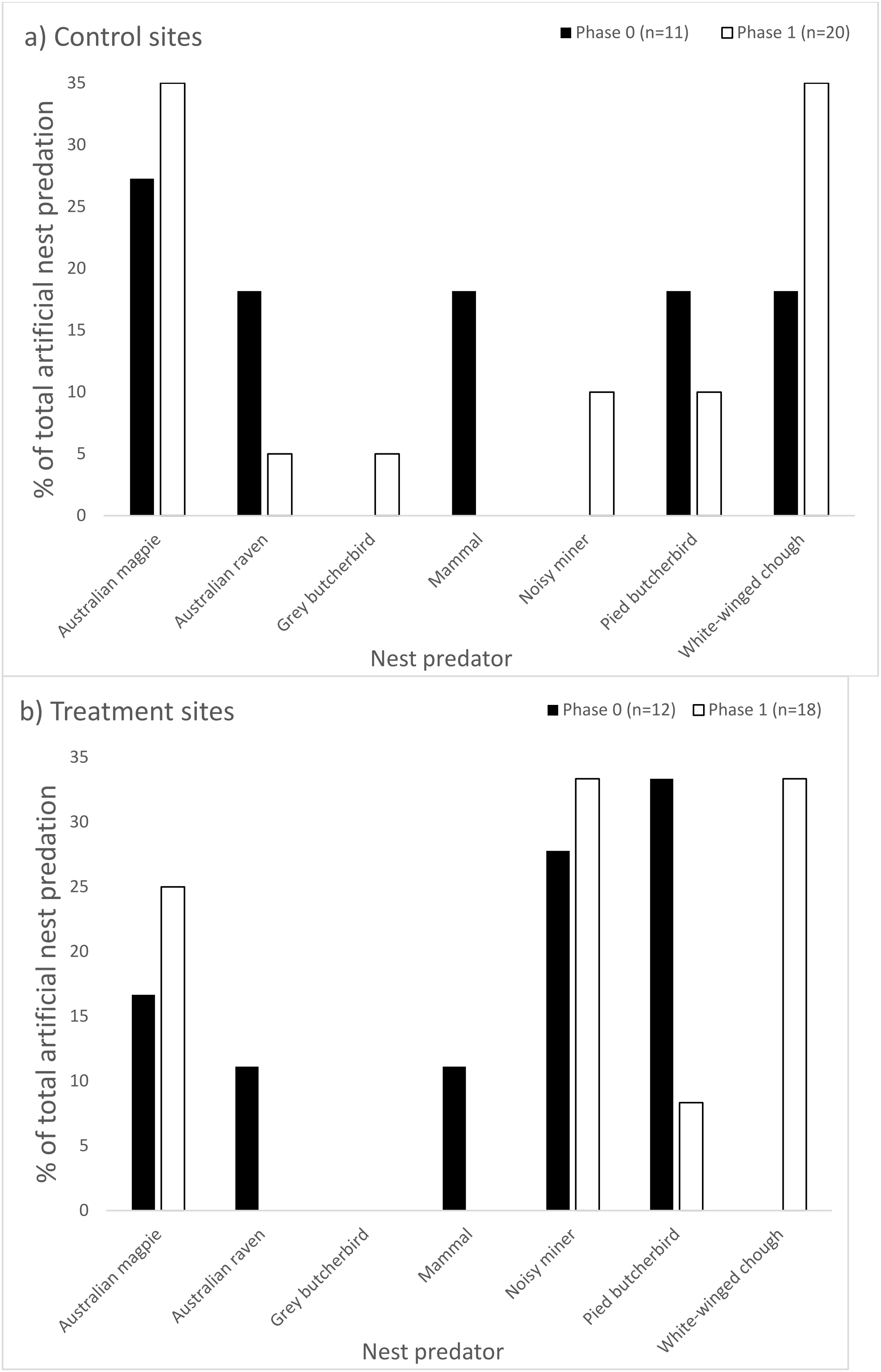

Figure S4. Contribution of nest predators to total artificial nest predation in treatment and control sites respectively

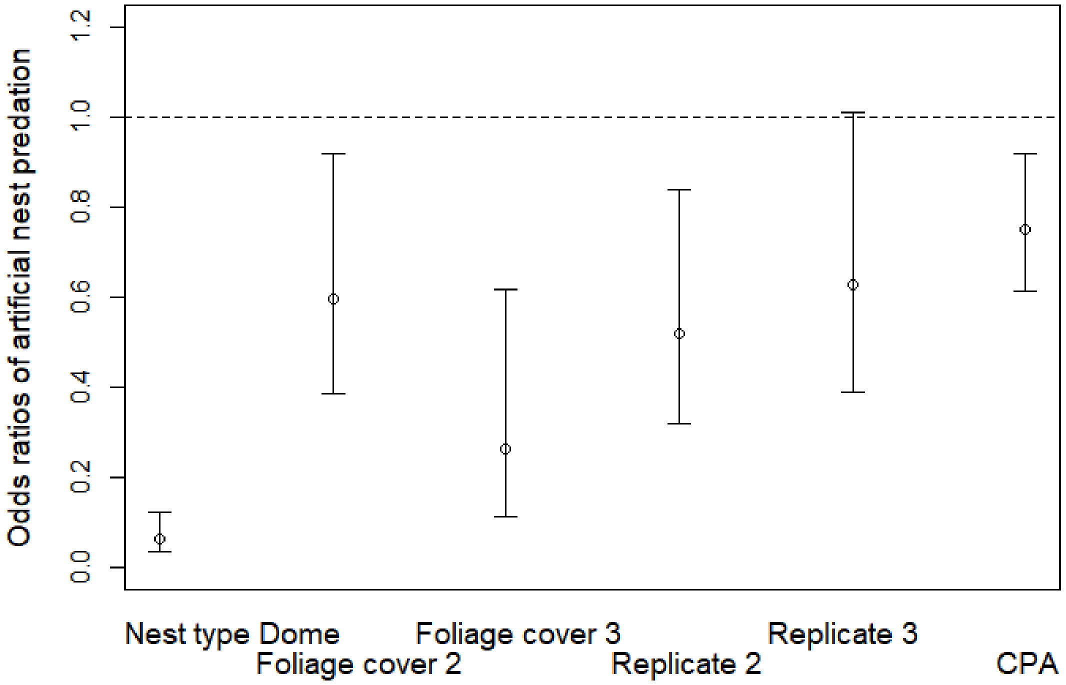

Figure S5. Effects of other significant explanatory variables on odds ratios of artificial nest predation. Odds ratios of nest predation for categorical variables are with respect to reference values Nest type cup, Foliage cover 1 and Replicate 1 respectively. For example, the plot for Nest type dome represents the ratio

$$\frac{Expected\ odds\ of\ artificial\ nest\ predation\ in\ dome\ nests}{Expected\ odds\ of\ artificial\ nest\ predation\ in\ cup\ nests}$$

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.

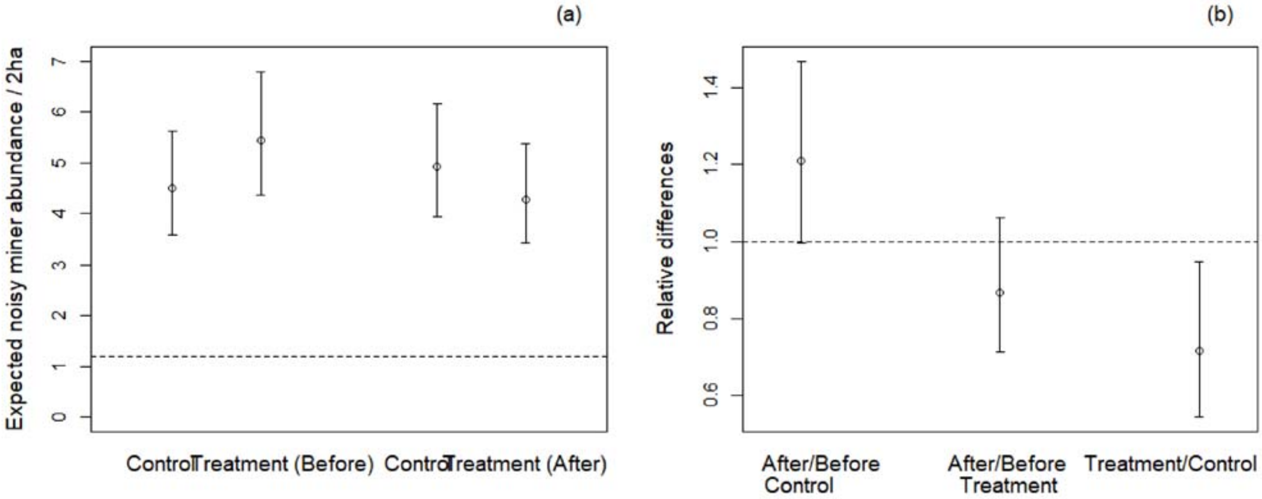

Figure S6. (a) Expected noisy miner abundances over the two breeding seasons of the study, with 95% confidence intervals. The dotted line at 1.2 birds/2ha is the impact threshold of noisy miner abundance on species assemblages (Thomson et al 2015). (b) Relative differences in expected noisy miner abundance 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_5FoliageCover3 + β_6 NestType + β_7 CPA + β_8 Replicate 2 + β_9 Replicate 3 + β_{10}Phase:NestType

Table S4. Using addition of logs to calculate ln expected odds of ANP for phase, treatment and phase:treatment interaction, assuming constant values for other model variables

	Control	**Treatment**
Phase 0 (before cull)	(β_0)	$(\beta_0 + \beta_1)$
Phase 1 (after cull)	$(\beta_0 + \beta_2)$	$(\beta_0 + \beta_1 + \beta_2 + \beta_3)$

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:

$$Relative\ \ change\ in\ expected\ odds\ of\ ANP\ = \frac{Expected\ odds\ after\ cull}{Expected\ odds\ before\ cull}$$

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:

$$Relative\ difference\ between\ change\ in\ expected\ odds\ \ \text{in treatment and control sites} = \frac{\frac{Expected\ odds\ after\ cull}{Expected\ odds\ before\ cull}\ (Treatment)}{\frac{Expected\ odds\ after\ cull}{Expected\ odds\ before\ cull}\ (Control)}$$

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

Worked example (using best model):

Table S5. Model output

Predictor	**Coefficient estimate (logit link)**
Intercept	1.34
Treatment	0.04

Phase	-0.48
Treatment:phase	-0.32

Table S6: Calculating ln expected odds ANP by treatment and phase using addition of logs (with exponentiated values in brackets) (see Figure 3(a), main document)

	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)

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 changes in Treatment to change in Control = 0.45/0.61 = 0.74 (see Figure 3(b), main document)

Table S7. 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

Table S8. Summary of best candidate models produced by the R package *MuMIn* which included the BACI base model (Treatment, Phase, Treatment:Phase).

Model	**AIC**	**ΔAIC**	**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 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