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Revegetation and reproduction: Do restoration plantings in agricultural landscapes support breeding populations of woodland birds?

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Our research is novel in its use of a mechanistic approach to assess the effectiveness of restoration plantings as a conservation strategy. We highlight the value of small habitat patches for threatened and declining avifauna.

Author contributions: DJB, JCP and DBL conceptualised the study and designed the experiment. DJB conducted the fieldwork, analysed the data, and wrote the manuscript. JCP, KI and DBL provided advice on data analysis and helped edit the manuscript.

Abstract

Restoration plantings are frequently occupied by native wildlife, but little is known about how planting attributes influence breeding by, and persistence of, fauna populations. We monitored breeding success of woodland birds in restoration plantings in a fragmented agricultural landscape in south-eastern Australia. We documented nest fate and daily nest survival (DSR) in plantings and remnant woodland sites. We analysed the influence on breeding success of patch attributes (size, shape, type) compared to other potentially influential predictors such as nest-site and microhabitat variables. We found that, in general, patch attributes did not play a significant role in determining breeding success for woodland birds. However, we examined a subset of species of conservation concern, and found higher DSR for these species in restoration plantings than in similarly-sized woodland remnants. We also found negative effects of patch size and linearity on DSR in species of conservation concern. The primary cause of nest failure was predation (91%). We used camera trap imagery to identify the most common nest-predators in our study sites: native predatory bird species, and the introduced red fox (*Vulpes vulpes*). Our findings are further evidence of the value of restoration plantings and small habitat patches for bird populations in fragmented agricultural landscapes. We recommend controlling for foxes to maximise the likelihood that restoration plantings and other woodland patches in Australia support breeding populations of woodland birds. More broadly, our study highlights the importance of taking a detailed, population-oriented approach to understanding factors that influence habitat suitability for fauna of conservation concern.

Keywords: revegetation, temperate woodland, SLOSS, population dynamics

1 Introduction

Habitat loss due to agricultural expansion is a key threat to biodiversity in many parts of the world (Maxwell et al. 2016; Egli et al. 2018). Ongoing loss of habitat in fragmented agricultural landscapes is making it increasingly difficult for many organisms to persist and maintain viable populations (Bennett et al. 2015; Haddad et al. 2015; Stanton et al. 2018). In an attempt to address these problems, there are increasing efforts to replant native vegetation in agricultural landscapes in many parts of the world. Ecological tree plantings – hereafter referred to as "restoration plantings" – collectively comprise millions of hectares of planted vegetation, costing billions of dollars to establish and maintain (Kimball et al. 2015; Crouzeilles et al. 2016). They are often implemented as a specific conservation strategy to replace lost habitat for threatened and declining fauna (McAlpine et al. 2016; Catterall 2018; Lindenmayer et al. 2018a). For example, in south-eastern Australia, over 90% of box-gum grassy woodland habitat has been lost (Thiele and Prober 2000), and woodland birds in this region have suffered substantial population declines (Barrett et al. 2007; Rayner et al. 2014). Consequently, woodland birds are frequently considered among the key beneficiaries of restoration plantings in south-eastern Australia (Belder et al. 2018).

There is evidence suggesting that many species of woodland bird will readily occupy restoration plantings (Barrett et al. 2008; Lindenmayer et al. 2010; Debus et al. 2017). Studies examining woodland bird responses to restoration plantings typically use pattern data such as presence and abundance to infer habitat quality. Previous research has offered insights into colonisation and extinction patterns (Barrett et al. 2008; Mortelliti and Lindenmayer 2015), changes in bird community composition in plantings over time (Mac Nally 2008; Lindenmayer et al. 2016, 2018c; Debus et al. 2017), and occupancy trends relating to site type, habitat structure, and composition (Martin et al. 2011; Munro et al. 2011; Ikin et al. 2018). However, do patch attributes have the same influence on breeding success as they do on site occupancy? Few studies have investigated breeding success in restoration plantings, and little is known about the role of restoration plantings in supporting successful breeding by woodland birds.

The presence of a species in a restoration planting does not necessarily mean that the site is supporting successful breeding of that species. Previous work has found that the relative abundance of woodland bird species is not necessarily correlated with their degree of breeding activity (Belder et al. 2019). For restoration plantings to support breeding populations of woodland birds, they must provide adequate resources and quality habitat to encourage persistence of individuals in a site, and to enable resident individuals to breed successfully (Arlt and Pärt 2007; Flockhart et al. 2016). This is an important outcome if restoration plantings are to be widely implemented as a conservation strategy (Ruiz-Jaen and Aide 2005).

In this study, we focus on breeding success as an indicator of habitat quality in restoration plantings and remnant woodland patches. Breeding success is a key measure of the productivity and quality of a habitat patch (Hinsley et al. 2008; Milligan and Dickinson 2016). By assessing whether successful breeding is occurring, we can begin to assess the extent to which a habitat patch is supporting the species that it is intended to help conserve. Moreover, identifying site attributes (e.g. size, shape) that best support successful breeding facilitates conservation planning, and has the potential to improve the cost-effectiveness of restoration plantings as a conservation strategy.

It is also important to identify the most common causes of breeding failure in restoration plantings. For example, low nesting success could be due to an introduced predator that thrives in fragmented agricultural landscapes, such as the red fox (*Vulpes vulpes*) in Australia (Braysher 2017). If this is the case, then an otherwise good quality restoration planting may never support species that are vulnerable to fox predation. However, this type of threat, once identified, could be readily addressed in management plans. Conversely, if nest predation is low but birds are abandoning nests or failing to fledge their young, it may indicate that resource limitation is the primary factor influencing breeding success and survival (Zanette et al. 2000). In this case, more detailed studies might establish what is driving resource limitation. For example, a lack of suitable nesting sites (exposure, competition), food shortage, or perhaps inefficient foraging strategies due to home ranges that are constrained by patch geometry or landscape context.

1.1 Research objectives

The primary aim of this study was to determine whether restoration plantings are able to support breeding populations of woodland birds. We used two different indicators of breeding success: nest fate and daily nest survival. Specifically, we posed the following three questions:

Question 1. How does breeding success in restoration plantings compare to breeding success in remnant woodland patches?

We compared breeding success (nest fate and daily nest survival) in restoration plantings and similarly-sized woodland remnants. We used larger woodland remnants, such as travelling stock reserves, as “reference” sites. Belder *et al.* (2019) found equal levels of breeding activity in restoration plantings and woodland remnants in the study area. We therefore predicted that breeding success in plantings would be similar to that in remnants.

Question 2. Are patch attributes such as size, shape and type important determinants of breeding success in plantings and remnant woodland patches?

We used a model selection approach to compare the influence of patch attributes (size, shape, type) with other variables that may influence breeding success, including nest-site variables (distance to edge of patch, height off ground, concealment), and microhabitat variables (shrub cover, ground layer composition). A previous study by Belder *et al.* (2019) identified a negative relationship between patch size and breeding activity, and a positive relationship between planting age and breeding activity. We expected these findings to be reflected in our study of breeding success, and postulated that patch attributes would significantly influence breeding success.

Question 3. What are the primary causes of nest failure in restoration plantings and woodland remnants?

We sought to identify the reasons for nest failure in restoration plantings, and establish whether the same processes are responsible for nest failure in woodland remnants. We predicted that predation would be the leading cause of nest failure in all sites, as it is the primary driver of nest failure in most bird communities (Belder et al. 2018). We also sought to quantify whether major nest-predators differ between patch types. Based on research conducted in a similar study region (Okada et al. 2017), and a recent review of nest-predators in Australia (Fulton 2019), we expected the dominant predators of woodland bird nests to be predatory bird species, including ravens (*Corvus* spp), butcherbirds (*Cracticus* spp), and currawongs (*Strepera* spp). We also expected the eastern brown snake (*Pseudonaja textilis*) to be a common nest-predator in restoration plantings, as they have been detected more frequently in plantings than in similarly-sized woodland remnants in our study region (Cunningham et al. 2007). Snakes have been identified as important nest-predators in Australia (Fulton 2019) and internationally (Weatherhead and Blouin-Demers 2004).

1.2 Approach

Our study was conducted over two breeding seasons and used real, active bird nests to quantify breeding success and nest-predation. The majority of previous studies in Australian landscapes, including in our study region, have used indicators of breeding activity as a proxy for breeding success (Barrett et al. 2008; Selwood et al. 2009; Mac Nally et al. 2010; Belder et al. 2019). While such indirect measures are an important step away from traditional diversity and abundance measures, they cannot accurately represent breeding success or identify reasons for breeding failure. We document, for the first time, nesting success, daily nest survival, and primary predators of woodland birds breeding in restoration plantings in a fragmented agricultural landscape.

2 Materials and Methods

2.1 Study area

We conducted our study in the South-west Slopes bioregion of New South Wales, Australia. The region is part of Australia's sheep-wheat belt and has been extensively cleared of native vegetation, with as little as 0.1% of the original temperate woodland remaining in intact condition (Thiele and Prober 2000). Remnant patches are predominantly white box (*Eucalyptus albens*) / yellow box (*E. melliodora*) / Blakely's red gum (*E. blakelyi*) grassy woodland, a critically-endangered ecological community (NSW OEH 2016). Patches of red stringybark (*E. macrorhyncha*) woodland and mugga ironbark (*E. sideroxylon*) woodland are also present.

2.2 Study sites

We used spring bird survey data collected over 12 years (see Lindenmayer et al. 2018c) to select a subset of 21 long-term monitoring sites: 12 plantings (1.3-7.7 ha), six similarly-sized woodland remnants (2.1-5.8 ha), and three large, intact remnants ("reference" sites >44 ha) (Figure 1). Plantings were aged between 12 and 25 years. We attempted to control for the effects of competitive exclusion by selecting sites that did not have a history of occupancy by the noisy miner (*Manorina melanocephala*). Details regarding study site selection are described in Belder *et al.* (2019).

2.3 Nest searches

We conducted fixed time-per-unit-area surveys (one hour per hectare) to locate nests in study sites over two breeding seasons. We completed two rounds of surveys (October and November) in 2015, and three rounds (September, October, November) in 2016. We searched sites systematically, with search areas designated by size and shape of sites. For sites with a total area less than 3 ha, we searched 1.3 ha within the site – this was equivalent to the size of the smallest site in the study. For sites with a total area greater than 3 ha, we searched 3 ha within the site. We surveyed block sites in a grid fashion, and linear sites along their length until we had searched the desired area (i.e. 1.3 ha or 3 ha). Due to the large geographic spread of sites, we were unable to completely randomise the order of site surveys during each round. However, we ensured that sites were not consistently surveyed at the same time of day. Sites were surveyed at any time of day from dawn to dusk, except during November 2016, when sites were surveyed only in the four hours post-sunrise and pre-sunset.

2.4 Nest monitoring

Once a nest was located, we used flagging tape to mark its position (near to but not at the nest to avoid attracting the attention of predators) and recorded its location using a handheld GPS. Depending on accessibility, we determined the status (i.e. the stage of development) of the nest at discovery by either manual inspection or through observations of parental behaviour. Some nests required multiple visits on different days to ascertain status. We conducted regular checks in person to verify status – every 7-10 days in 2015, and every 3-5 days in 2016. We inspected nests manually or used a nest inspection tool (endoscopy-type camera for dome nests, and mirror on an extendible pole for open cup nests). For nests that were out of arm's reach or could not be reached by extendible pole, we used behavioural observations to determine status. We observed nests for up to 30 minutes, or until we recorded activity at the nest and could verify the status. If we could not determine the status within the 30 minute observation period, we repeated the observation at the next scheduled visit (3-5 days later in 2016). If we did not record activity in three consecutive visits, we assumed the nest was no longer active. In the later stages of nesting (i.e. when the nest was estimated to be within 5 days of fledging), we did not approach the nest, and used only behavioural observations to determine status. This was to minimise the risk of premature fledging. We considered a nesting attempt to have succeeded if at least one chick fledged.

Where possible, we used fixed motion-sensing wildlife cameras to monitor nests, with the primary aim of detecting nest predation. We used a combination of Bushnell Trophy HD, UOVision UV565HD, and HCO ScoutGuard SG560K black flash cameras. All cameras are triggered by motion within the field of view. To reduce the incidence of false triggers (e.g. by wind-blown foliage), we set camera sensitivity to “low”. We were able to use nest cameras for nests at heights of up to 6 m.

2.5 Nest site measurements and microhabitat surveys

For all nests, we recorded a GPS location (accurate to the nearest 2 m), the height of the nest above ground, and the substrate (foliage, branch, woody debris, etc.) in which the nest was built. For nests in the 2016 breeding season, we also recorded concealment (visually estimated at a distance of approximately 10 m, and to the nearest 5%). We used ArcMap (ESRI 2011) to calculate the distance of each nest to the nearest patch edge. Where relevant, we also recorded the plant species in which nests were built.

For nests in the 2016 breeding season, we collected microhabitat data around the nest site. We conducted microhabitat surveys when the nest was no longer active (either fledged or failed). At each nest, we used a tape measure to mark out a quadrat measuring 25 m along its diagonal, with the nest at its centre. The two diagonals were aligned north-south and east-west. We visually estimated the proportion of ground cover (to the nearest 1%) and midstorey cover (to the nearest 5%). We chose these microhabitat variables as multiple studies have documented their influence on site occupancy by woodland birds (Seddon et al. 2003; Antos and Bennett 2006; Montague-Drake et al. 2009; Munro et al. 2011).

2.6 Statistical analyses

We used a model selection approach (Burnham and Anderson 2004) to investigate the effects of patch-level, nest-level, and microhabitat variables on nest fate and daily nest survival (Table 1). For clarity, and to address inconsistencies with data collection between years, we modelled data only from nests monitored in 2016. We used generalised linear mixed effects regression models with study site as a random effect. Our response variables were nest fate (binary, where success = 0 and fail = 1), and daily nest survival (DSR). For nest fate and DSR analyses, we excluded nests for which the failure date was uncertain (to the nearest five days), most of which were classified as "abandoned". We included these nests, along with those monitored in 2015, when calculating the total proportion of successful nests, and we report these results in the *General findings* section of our Results. Due to inherent differences in nest survival, we analysed dome-nesters and cup-nesters separately. We had sufficient data to individually examine one dome-nesting species: the superb fairywren (*Malurus cyaneus*), and one cup-nesting species: the willie wagtail (*Rhipidura leucophrys*). We also examined a subset of dome-nesting species of conservation concern (Appendix 1). We did not include nests of introduced species in our study.

We used a comparative model selection approach, in which we modelled combinations (sets) of variables and used Akaike's Information Criterion to determine which variables best predicted nest fate and DSR:

1. Patch attributes: type, size (ha), shape (calculated as perimeter/width)
2. Nest site attributes: height above ground, distance to edge of patch, concealment

3. Microhabitat variables: shrub cover and ground layer composition within 20 m of the nest.

We included date of nest discovery (DATE) as an explanatory variable in all models, as preliminary analyses indicated that date within the breeding season was a significant influence on breeding success. For the first two sets of variables, we fitted models with the variables of interest plus interaction terms. For models including microhabitat variables, we did not include interaction terms. For daily nest survival model selection, we included a model that assumed constant nest survival (null model). We ranked candidate models using Akaike's Information Criterion corrected for small sample sizes (AIC_c). We considered models with $\Delta AIC_c \leq 2$ as top-ranked models (Burnham and Anderson 2004).

When reporting DSR results, we provide both the sample size (n) and effective sample size (n_{ess}) (Rotella et al. 2004; Shaffer and Thompson 2007). Effective sample size is equal to the number of known days survived for each nest plus the number of intervals in which a nest failed (Rotella et al. 2004). For example, a nest that survived for 10 days and then failed between day 10 and day 13 contributes 11 to the study's effective sample size.

We used the packages 'lme4' (Bates et al. 2015) and 'MuMIn' (Bartoń 2018) in R version 3.5.2 (R Core Team 2019) to fit and select models for FATE. For DSR calculation and model selection, we used Program MARK (White and Burnham 1999) via the R package 'RMark' (Laake 2003). To calculate model estimates and confidence intervals, we used the R packages 'dplyr' (Wickham et al. 2019) for FATE and 'RMark' for DSR.

Prior to fitting models, we checked all explanatory variables for multi-collinearity using variance inflation factors. We corrected for multi-collinearity by removing large reference sites from models that included both size and type (site type was significantly correlated with site size due to the comparatively large size of reference sites). That is, we included data only from plantings and similarly-sized woodland remnants when modelling our response variable against site size and shape. We also scaled and centred our continuous predictor variables for generalised linear mixed modelling.

3 Results

3.1 General

We located 324 woodland bird nests over the course of the two years of field study: 89 in 2015, and 235 in 2016. Of these, we were able to successfully track the fate of 222 nests, or 69% of the total number of nests. Of the nests that were tracked successfully, 129 were in plantings (12 sites), 45 were in remnants (six sites), and 48 were in large reference sites (three sites). We analysed nests from 24 different woodland bird species: 11 dome-nesters and 13 cup-nesters (Appendix 1).

Nests were predominately in the lower strata. Mean nest height was 2.2 m (SE=0.16 m). Cup nests in large reference sites were significantly higher on average than in restoration plantings and similarly-sized woodland remnants ($p<0.0001$). Site type did not influence nest height for dome nests.

Mean nest success (succeed vs. fail) across all nest types was 33.8%. Success rates were 29.6% for cup-nesters and 38.1% for dome-nesters (Figure 2).

We calculated daily nest survival for 107 dome nests (n_{ess} = 2134) and 50 cup nests (n_{ess} = 599) (Table 2). As the breeding season progressed, DSR decreased for dome-nesters but increased for cup-nesters (Figure 3).

Dome-nesters frequently nested in kangaroo thorn (*Acacia paradoxa*), red box (*Eucalyptus polyanthemos*), Blakely’s red gum, and *Phalaris aquatica* (an introduced grass species). Plant species used frequently by cup-nesters included Blakely’s red gum, white box, and kangaroo thorn. Both cup-nesters and dome-nesters nested most often in trees. Dome-nesters also frequently nested in shrubs and woody debris. Cup-nesters rarely built nests in shrubs or woody debris.

We found that in linear sites that were oriented north-south, it was common for nests to be located on the eastern side of the site. This meant that nests were exposed to the warmth of the early morning sun but protected from overheating in the afternoon.

3.2 Model selection results

When analysing nest fate, we found that the null model was retained for every assemblage and species of interest, and in every iteration of our analyses (Appendix 2–4). That is, none of the predictors in our candidate models explained the variation in nest fate. We found that analysing daily nest survival produced more conclusive results. When all sites were included (plantings, remnants, large reference sites), the null model was again retained in every instance (Appendix 5). We found that candidate models performed better against the null model when large reference sites were excluded (Table 3). We did not find any conclusive results when analyses were restricted to restoration plantings (Appendix 6). Note that we had sufficient data to examine only dome-nesters and the superb fairy-wren in restoration plantings.

3.3 Effects of patch type

Daily nest survival for species of conservation concern was higher in plantings than in similarly-sized woodland remnants (Table 4). Patch type did not influence daily nest survival for any other groups of interest. We did not identify any effect of patch type on nest fate for woodland birds in our study (Appendix 2, Appendix 3).

3.4 *Importance of patch attributes*

For species of conservation concern, daily nest survival in plantings and similarly-sized woodland remnants was better predicted by patch attributes than by nest-site or microhabitat variables (Table 3). This was the only instance in which patch attributes outperformed the null model. In addition to the aforementioned effect of patch type, we found that daily nest survival for species of conservation concern decreased with increasing patch size (Table 4). We also found a negative effect of linearity, with lower daily nest survival in more linear sites.

Daily nest survival for cup-nesting species in plantings and similarly-sized remnants was best predicted by nest-site variables (Table 3). We found a negative effect of nest height – nests situated higher above the ground were associated with lower survival probabilities (Table 5). Effects estimates for other variables in the model had large standard errors, and were therefore not interpretable.

Microhabitat variables were of little importance in determining breeding success of woodland birds in our study (Table 3, Appendix 2–7). Likewise, the age of restoration plantings did not contribute to predicting either nest fate or daily nest survival (Appendix 4, 7).

3.5 *Causes of nest failure*

The primary cause of nest failure was predation, which we identified as the cause of 91% of failed nests. This did not differ significantly between plantings, remnants, or large reference sites. Most other nest failures were attributed to abandonment, usually during the egg stage.

3.6 *Nest-predators*

We monitored 85 nests with cameras, and analysed a total of 308,249 camera trap images. Predation events recorded during our study were most often perpetrated by generalist avian predators, including ravens, the pied currawong (*Strepera graculina*), and pied butcherbird

(*Cracticus torquatus*) (Table 6). The next most common nest-predator (and the most damaging individual species) identified in restoration plantings and woodland remnants was the red fox (Table 6; Appendix 7). Foxes targeted nests close to the ground, including those of the superb fairywren (Table 6). We also recorded some unexpected nest-predators, including the white-browed babbler (*Pomatostomus superciliosus*) (see Belder 2018), and common ringtail possum (*Pseudocheirus peregrinus*). The eastern brown snake was recorded as a nest-predator in a restoration planting on one occasion (Table 6).

4 Discussion

Our results are empirical evidence that restoration plantings provide suitable breeding habitat for woodland birds, and may eclipse remnant patches in supporting successful breeding of woodland birds. We found that woodland birds bred at least as successfully in restoration plantings as they did in remnant woodland patches and large reference sites. Indeed, species of conservation concern were more likely to breed successfully in restoration plantings than in remnant woodland patches. Other notable findings included negative effects of both patch size and linearity on daily nest survival for species of conservation concern.

Nest survival as measured in our study was somewhat lower than expected, particularly for cup-nesting species (29.6% for cup-nesting species and 38.1% for dome-nesting species). Nest survival for Australian songbirds of the families included in our study average 42.2% for dome-nesting species and 37.7% for cup-nesting species (Remeš et al. 2012). This may indicate that habitat suitability of restoration plantings and remnant patches in our study region is lower for cup-nesters than it is for dome-nesters. Many cup-nesting species are perch-and-pounce ground-foraging species, including the willie wagtail and various robins (Petroicidae). Species in the latter family have been identified as susceptible to population decline, and careful management of the ground layer has been recommended to improve habitat suitability for these species (Recher et al. 2002; Antos and Bennett 2006; Montague-Drake et al. 2009).

A decline in breeding success over the course of the breeding season, as documented for the dome-nester assemblage, is consistent with patterns observed for many bird species worldwide (Arnold et al. 2004). The positive effect of date on DSR that we recorded for cup-nesters was unexpected. Potential explanations include more stable weather conditions later in the season, lower predation risk (particularly by avian predators), or changes in microhabitat variables such as grass cover over the course of the breeding season.

Belder *et al.* (2019) documented equivalent levels of breeding activity in restoration plantings and woodland remnants, including for species of conservation concern. Our findings regarding breeding success are quantitative evidence that restoration plantings provide valuable habitat in which threatened and declining bird species can persist and breed. They also potentially highlight a need to improve the quality of woodland remnants through restorative actions such as excluding stock or replanting the shrub layer. Some species of conservation concern, such as the brown treecreeper (*Climacteris picumnus*), rely on habitat features that are present in woodland remnants but take decades to develop in restoration plantings (Vesk et al. 2008). It is for this reason that restoration plantings should be considered complementary to, and not a replacement for, remnant woodland (Cunningham et al. 2008; Lindenmayer et al. 2018d; Ikin et al. 2018).

Previous studies have documented a positive relationship between patch size and reproductive output in birds (e.g. Burke and Nol 2000; Zanette *et al.* 2000; Zanette and Jenkins 2000; Zanette 2001). This has led to the prevalent view that larger patches are more valuable for woodland birds in fragmented agricultural landscapes. However, Belder *et al.* (2019) found that breeding activity in the South-west Slopes bioregion decreased with increasing patch size. The results of the present study substantiate this finding. Previous research has described the value of small patches for sustaining wildlife populations (Tulloch et al. 2016; Lindenmayer 2019; Wintle et al. 2019). Our study provides direct evidence that woodland birds are able to breed successfully in small habitat patches. Possible reasons for greater success in small patches include lower abundances of predators and brood parasites in small patches, the dominance of edge-specialists and habitat generalists, and concentration effects (Belder et al. 2019).

While linear patches may provide suitable habitat for some species (as evidenced by our general finding of little influence of linearity on breeding success), our results indicate that species of conservation concern may benefit more from block-shaped sites. This may be one reason why linear sites have previously been found to contain a less diverse species assemblage than block-shaped sites (Kinross 2004; Lindenmayer et al. 2010, 2018b). This is of interest for conservation planning, as it highlights the need to take into account the habitat requirements of different species and assemblages when designing revegetation programs.

The presence of nest height as an explanatory variable in top models for cup-nesters may be a reflection of the dominant predators in the study region – open cup-nests are frequently targeted by avian predators (Okada et al. 2019), which may more easily locate these nests higher up in the canopy. We did not find any evidence that the distance of a nest to the nearest patch edge influenced breeding success. This is suggestive of a lack of edge-effects, which have been thought to decrease the value of small and/or linear habitat patches for birds in fragmented agricultural landscapes (Ewers and Didham 2007; King et al. 2009). However, as discussed earlier, our results showed that species of conservation concern bred more successfully in sites of decreasing linearity. One potential explanation is that linear sites do not facilitate optimal central place foraging, since nesting birds must expend more energy traversing a linear home range than one that is more uniform in shape (Andersson 1978; Bovet and Benhamou 1991; Rosenberg and McKelvey 2016).

It is somewhat surprising that microhabitat variables and planting age contributed little to explaining breeding success in our study. Previous research has documented the influence of variables such as shrub cover and ground layer complexity on site occupancy by woodland birds (Seddon et al. 2003; Antos and Bennett 2006; Montague-Drake et al. 2009; Munro et al. 2011). Belder *et al.* (2019) also reported increased breeding activity of woodland birds in younger restoration plantings, which the authors postulated was due to a diversity of nest-site choices and foraging opportunities associated with the presence of an intact shrub layer. It is possible that microhabitat variables other than the ones included in this study may have had a greater influence on breeding success.

The high nest-predation rate we recorded during our study is not unprecedented (see Zanette and Jenkins 2000; Guppy et al. 2017), but it is nonetheless of concern for the persistence of woodland bird populations in our study region. Generalist avian predators, including corvids, are often considered among species that have benefited from land clearing and habitat fragmentation in agricultural landscapes worldwide (Andrén 1992; Ford et al. 2001; Fuller et al. 2005). Invasive predators, including foxes, also benefit from increasing agricultural land-use (Graham et al. 2012). Zanette and Jenkins (2000) suggest that decreasing forest cover at the landscape scale is a key factor that has led to increased incidence of nest-predation. Measuring landscape-scale vegetation cover was outside the scope of our study, but more than five million hectares of white box / yellow box / Blakely's red gum grassy woodland has been cleared since European settlement, and less than 10% of this ecological community remains across its historic range (Manning et al. 2011). The low levels of landscape vegetation cover in our study region may be a significant influence on woodland bird population dynamics.

Prior to commencing this study, we predicted that predatory bird species and the eastern brown snake would be the dominant nest-predators in our study sites. While avian predators such as ravens and butcherbirds were indeed responsible for the majority of predation events captured during our study, we also identified another common predator – the introduced red fox. The prevalence of foxes as nest-predators in restoration plantings is cause for concern, and may limit the habitat suitability of plantings for woodland birds that nest in the lower strata or on the ground. These include several threatened and declining species, such as the speckled warbler (*Pyrrholaemus sagittatus*).

4.1 Inferential limitations

Our study has revealed previously undocumented trends in woodland bird breeding success, and provided insights into the capacity of restoration plantings and small habitat patches to support woodland birds. We acknowledge a number of limitations pertaining to the present study, and communicate these here to assist with interpretation.

First, this study was conducted over a short duration. The first field season was a pilot study that enabled collection of nest fate data only, leaving one field season in which we could collect sufficiently detailed data to calculate daily nest survival. Caution is advised when extrapolating from studies of only a year duration (Maron et al. 2005). The field season on which a majority of the data in this paper are based coincided with a year of above average rainfall. Since the productivity of southern temperate woodlands is strongly linked to soil moisture (Watson 2011), it is possible that breeding success in our study region may ordinarily be lower than documented in our study.

Second, the presence of the noisy miner, a hyperaggressive native honeyeater, in fragmented agricultural landscapes is a key threatening process for many woodland bird species (Montague-Drake et al. 2011; Bennett et al. 2015; Maron et al. 2016). The noisy miner harasses small woodland birds, is a known nest-predator, and has been directly implicated in reduced breeding success of woodland bird species (Maron 2007; Maron et al. 2013; Bennett et al. 2015; Beggs et al. 2019). Our study was conducted in the absence of the noisy miner, but it is important to recognise that this species may be present and adversely affect breeding success of woodland birds in restoration plantings or other woodland patches.

4.2 Future research directions and management implications

We suggest that future research should focus on identifying the reasons for low breeding success in linear patches, particularly given the popularity of such configured habitat patches in agricultural landscapes. We also recommend more detailed studies on breeding success of individual species. In particular, it would be worth focusing on robins and other declining cup-nesting species to identify reasons for low nest survival and more frequent failure earlier in the breeding season (sensu Zanette et al. 2000). More extensive habitat surveys (as opposed to a focus on the immediate vicinity of the nest) might prove useful in assessing the influence of habitat variables on breeding success. In terms of management, we recommend controlling for foxes to maximise the likelihood that restoration plantings and other woodland patches support breeding populations of woodland birds.

There is still much to be learned about woodland bird population dynamics in restored landscapes, and in fragmented agricultural landscapes generally. We suggest that future studies on the responses of woodland birds (and other fauna) to conservation strategies move beyond pattern data and adopt more detailed, population-oriented approaches such as the one presented in our study. Future research should focus on aspects of habitat quality that are likely to influence population persistence, such as identifying the major threats to woodland bird breeding. We also suggest that future studies be undertaken over longer time periods, to capture inter-annual variation in breeding success and reproductive output. This is particularly relevant in large parts of Australia, where animal populations fluctuate in response to extreme interannual variations in climate and rainfall (Letnic and Dickman 2006; Burbidge and Fuller 2007). Basing management outcomes on multiple years of study is a crucial component of ongoing successful biodiversity conservation. It would be highly beneficial to include studies such as ours in long-term monitoring projects, so that community responses to environmental change can be documented. However, we acknowledge that monitoring breeding success is labour-intensive, time-consuming, and costly.

With the emergence of new wildlife monitoring technologies, including improvements in camera trap technology, we are hopeful that nest-monitoring will become easier and therefore more commonplace in bird breeding studies. A camera trapping method and/or software that could accurately and reliably determine key events in the nesting cycle (completion of building, egg-laying, hatching, nest predation, fledging, and abandonment) could revolutionise our ability to assess breeding success in studies worldwide. This would facilitate the incorporation of breeding studies into long-term monitoring projects, and importantly, in projects that aim to evaluate the success of conservation strategies.

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6 Conflicts of interest

The authors declare no conflicts of interest.

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Table 1 Linear mixed model parameters. The response variables are FATE and DSR, and all other variables are predictors.

Variable name	Response/predictor	Model set	Description
FATE	Response		Nest fate (a binary variable where 0 = survive and 1 = fail)
DSR	Response		Daily survival rate, calculated using Program MARK
DATE	Predictor		Julian date of nest discovery
TYPE	Predictor	Patch	Patch type (planting, remnant, reference)
SIZE	Predictor	Patch	Patch size (ha)
SHAPE	Predictor	Patch	Measure of patch shape, calculated as perimeter/width (m)
AGE	Predictor	Age	Age of planting at the commencement of the study (years)
HEIGHT	Predictor	Nest	Height of nest above ground (m)
DIST_EDGE	Predictor	Nest	Distance of nest to nearest patch edge (m)
CONCEALMENT	Predictor	Nest	Nest concealment, estimated at approx. 10 m from the nest (%)
BARE GROUND	Predictor	Microhabitat	Proportion of bare ground cover within 20 m of the nest
LEAF LITTER	Predictor	Microhabitat	Proportion of leaf litter cover within 20 m of the nest
GRASS	Predictor	Microhabitat	Proportion of exotic grass cover within 20 m of the nest
WOODY DEBRIS	Predictor	Microhabitat	Proportion of woody debris cover within 20 m of the nest
SHRUB COVER	Predictor	Microhabitat	Amount of midstorey shrub cover (%)

Table 2 Number of nests (n) and effective sample size (n_{ess}) used to calculate daily nest survival (DSR) for each subset of the woodland bird assemblage.

Subset	**Sites**	n	n_{ess}
dome	planting + remnant + reference	107	2134
	planting + remnant	86	1682
	planting	72	1393
cup	planting + remnant + reference	50	599
	planting + remnant	39	428
superb fairywren	planting + remnant + reference	56	1046
	planting + remnant	46	826
	planting	37	652
conservation concern	planting + remnant + reference	34	720
	planting + remnant	31	647

Table 3 Daily nest survival models for woodland birds in restoration plantings and similarly-sized woodland remnants (excluding large reference sites). Models are ranked by Akaike's Information Criterion corrected for small sample sizes (AIC_c).

Dome-nesters	npar	AIC_c	ΔAIC_c	AIC_w	Deviance
Constant	1	343.94	0.00	0.73	341.93
TYPE + SIZE + SHAPE + DATE	5	346.53	2.59	0.20	336.49
DIST_EDGE + CONCEALMENT + HEIGHT + DATE	5	348.82	4.88	0.06	338.78
GRASS + BARE GROUND + LEAF LITTER + WOODY DEBRIS + SHRUBS + DATE	7	352.06	8.12	0.01	337.99
Cup-nesters					
DIST_EDGE + CONCEALMENT + HEIGHT + DATE	5	134.88	0.00	0.75	124.74
Constant	1	137.74	2.86	0.18	135.73
TYPE + SIZE + SHAPE + DATE	5	140.18	5.29	0.05	130.03
GRASS + BARE GROUND + LEAF LITTER + WOODY DEBRIS + SHRUBS + DATE	7	142.46	7.57	0.02	128.19
Superb fairywren					
Constant	1	180.65	0.00	0.80	178.64
DIST_EDGE + CONCEALMENT + HEIGHT + DATE	5	184.06	3.41	0.14	173.98
TYPE + SIZE + SHAPE + DATE	5	186.51	5.86	0.04	176.44
GRASS + BARE GROUND + LEAF LITTER + WOODY DEBRIS + SHRUBS + DATE	7	189.24	8.59	0.01	175.10
Species of conservation concern					
TYPE + SIZE + SHAPE + DATE	5	122.98	0.00	0.73	112.89
Constant	1	125.54	2.56	0.20	123.53
DIST_EDGE + CONCEALMENT + HEIGHT + DATE	5	127.89	4.91	0.06	117.79
GRASS + BARE GROUND + LEAF LITTER + WOODY DEBRIS + SHRUBS + DATE	7	133.66	10.68	0.00	119.49

Table 4 Parameter estimates for daily nest survival models computed by Program MARK for species of conservation concern in restoration plantings and similarly-sized woodland remnants (n = 31, ESS = 647).

Parameter	Estimate (SE)
Intercept	4.77 (0.69)
TYPE (remnant)	–1.56 (0.97)
SIZE	–0.97 (0.34)
SHAPE	–0.57 (0.29)
DATE	–0.02 (0.01)

Table 5 Parameter estimates for daily nest survival modelled against nest-site variables for cup-nesting species in restoration plantings and similarly-sized woodland remnants (n = 39, ESS = 428).

Parameter	Estimate (SE)
Intercept	1.75 (0.53)
DIST_EDGE	0.18 (0.24)
CONCEALMENT	0.04 (0.23)
HEIGHT	–0.61 (0.28)
DATE	0.01 (0.01)

Table 6 Nest-predators identified from camera trap imagery of 85 monitored woodland bird nests in the South-west Slopes bioregion, NSW. Note that it was not possible to distinguish between Australian Raven (*Corvus coronoides*) and Little Raven (*C. mellori*) on camera trap imagery. Cattle and sheep are included as predators on the basis of camera trap imagery, but may have destroyed nests without consuming eggs or nestlings.

Common name	Species	Planting	Remnant	Reference	Total	Nest height (m)
*Red Fox	*Vulpes vulpes*	5	1	2	8	0–1.1
Australian/Little Raven	*Corvus* sp.	5		1	6	0.9–2.2
Pied Currawong	*Strepera graculina*	1		2	3	0.3–5.5
Pied Butcherbird	*Cracticus torquatus*		2		2	1.6–1.7
Brown Goshawk	*Accipiter fasciatus*	1			1	1.7
White-browed Babbler	*Pomatostomus superciliosus*	1			1	0.4
Australian Magpie	*Gymnorhina tibicen*			1	1	1.1
Common Brushtail Possum	*Trichosurus vulpecula*			1	1	0.1
Common Ringtail Possum	*Pseudocheirus peregrinus*			1	1	4.0
*Cattle	*Bos taurus*		1		1	0.3
*Sheep	*Ovus aries*			1	1	0.3
Eastern Brown Snake	*Pseudonaja textilis*	1			1	0.2
Eastern Blue-tongue Lizard	*Tiliqua scincoides*	1			1	0.2

*Introduced species

Figure 1

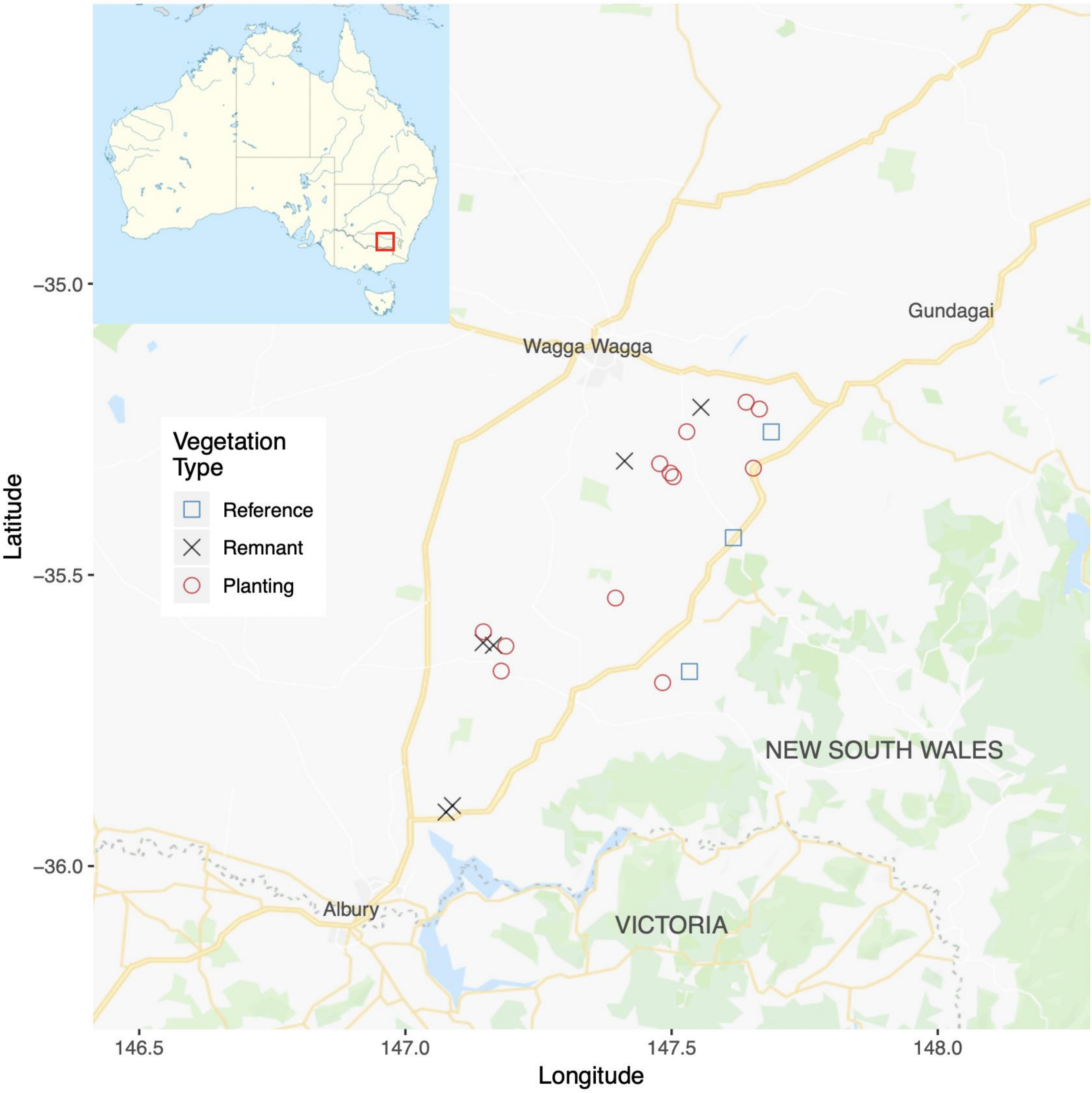
Vegetation Type
□ Reference
× Remnant
○ Planting
Gundagai
Wagga Wagga
NEW SOUTH WALES
VICTORIA
Albury
Latitude
−35.0
−35.5
−36.0
146.5
147.0
147.5
148.0
Longitude

Figure 2

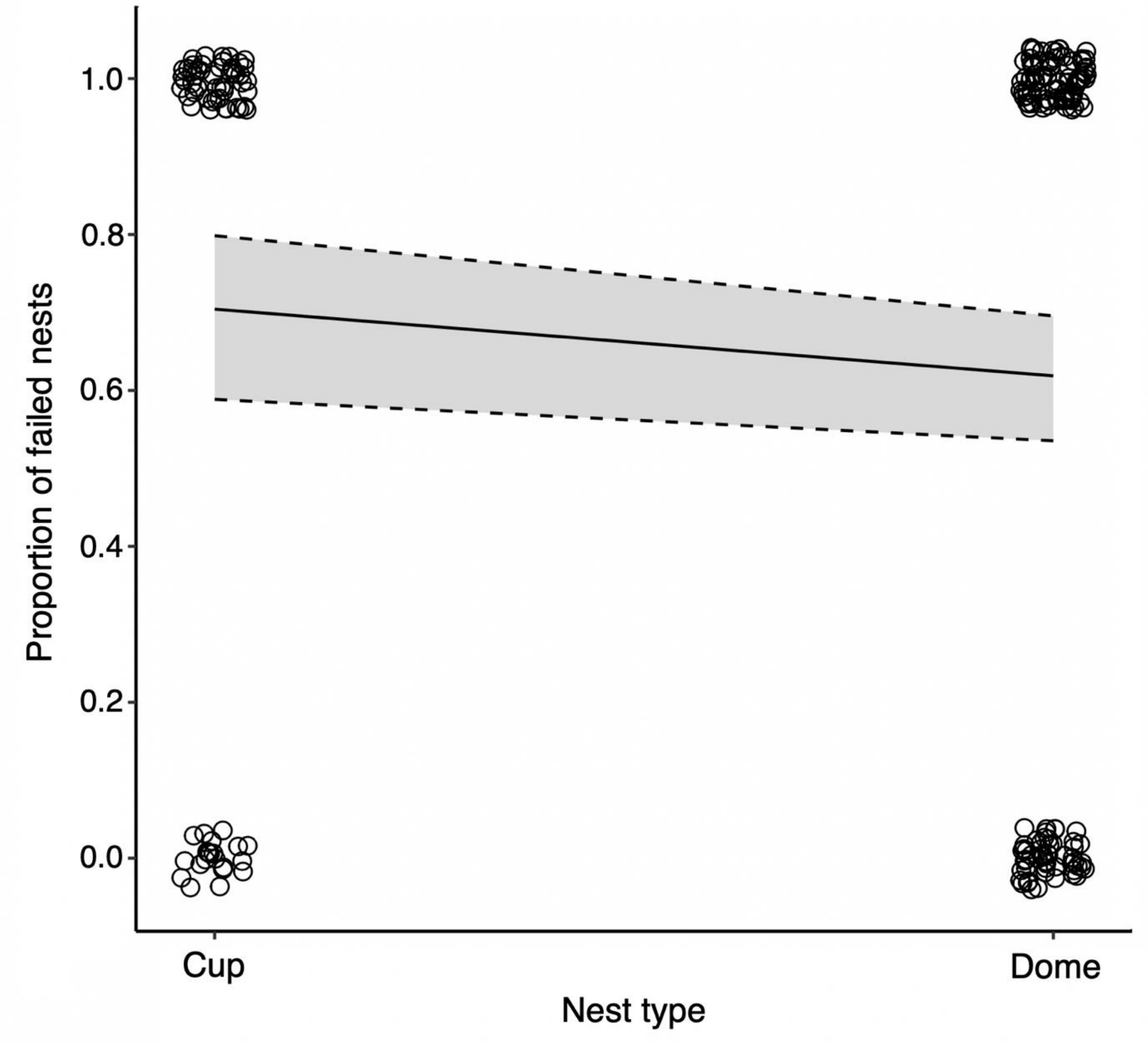
Proportion of failed nests
1.0
0.8
0.6
0.4
0.2
0.0
Cup
Dome
Nest type

Figure 3

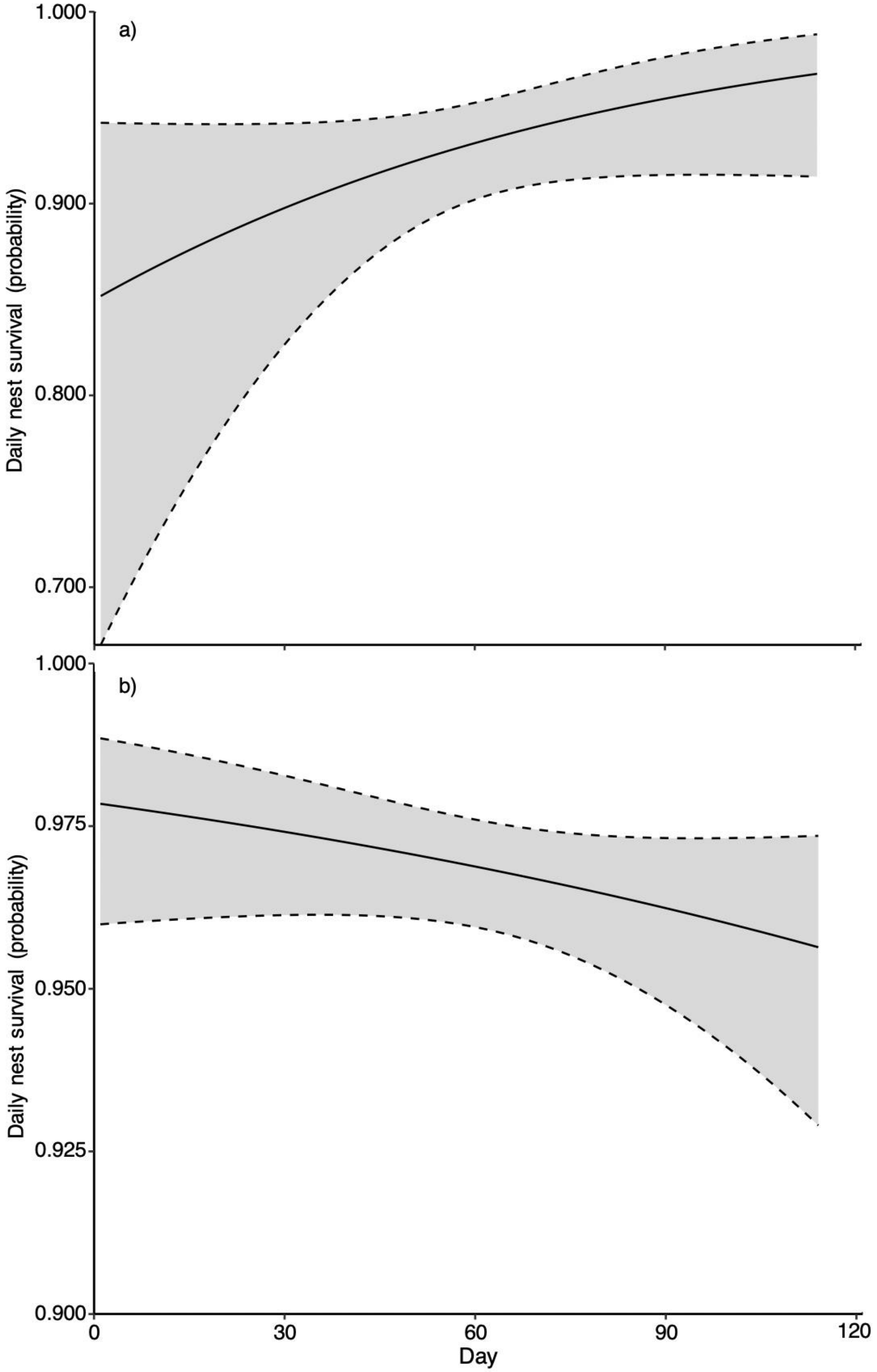
a)
b)
Daily nest survival (probability)
1.000
0.900
0.800
0.700
Daily nest survival (probability)
1.000
0.975
0.950
0.925
0.900
0
30
60
90
120
Day

Figure Legends

Figure 1 Map of study sites in the South-west Slopes bioregion of New South Wales, Australia. Map created using ggmap for R (Kahle and Wickham 2013).

Figure 2 Proportion of failed woodland bird nests according to nest type. Shaded areas indicate upper and lower 95% confidence intervals. Clustered points indicate frequency of success (0) and failure (1) for each nest type. Data from both 2015 and 2016 were modelled to produce estimates. Plot created using ggplot2 for R (Wickham 2016).

Figure 3 Daily nest survival of cup-nesting species (a) and dome-nesting species (b) over the course of the 2016 spring breeding season in the South-west Slopes bioregion, NSW. Probability refers to the likelihood of the nest surviving to the end of the study. Day 1 represents the first day of the study (the first day on which a nest could be discovered). Shaded areas indicate upper and lower 95% confidence intervals. Plot created using ggplot2 for R (Wickham 2016).