An ecological paradox: More woodland predators and less artificial nest predation in landscapes colonized by noisy miners

OLIVER ROBERTSON[1]*, MARTINE MARON[1] , YVONNE BUCKLEY[2,3], ALAN HOUSE[4], CLIVE MCALPINE[1,2]

[1]The University of Queensland, Landscape Ecology and Conservation Group, Centre of Spatial Environmental Research, School of Geography, Planning and Environmental Management, Brisbane, Australia.

[2]The University of Queensland, ARC Centre of Excellence in Environmental Decisions, Brisbane, Australia.

[3]The University of Queensland, School of Biological Sciences, Brisbane, Australia.

[4]Ecosure, Brisbane, Australia

*Corresponding author. School of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, Queensland 4067, Australia. E-mail: o.robertson@uq.edu.au. Phone: 3365 8340. Fax: 3365 6899

Running title: Artificial nests and the Additive Predation Model

Abstract

Many passerine bird populations, particularly those that have open-cup nests, are in decline in agricultural landscapes. Current theory suggests that an increase in habitat generalist predators in response to landscape change is partially responsible for these declines. However, empirical tests have failed to reach a consensus on how and through what mechanisms landscape change affects nest predation. We tested one hypothesis, the Additive Predation Model with an artificial nest experiment in fragmented landscapes in southern Queensland, Australia. We employed structural equation modelling of the influence of the relative density of woodland and habitat generalist predators and landscape features at the nest, site, patch and landscape scales on the probability of nest predation. We found little support for the Additive Predation Model, with no significant influence of the density of woodland predators on the probability of nest predation, although landscape features at different spatial scales were important. Within woodlands fragmented by agriculture in eastern Australia, the presence of noisy miner colonies appears to influence ecological processes important for nest predation such that the Additive Predation Model does not hold. In the absence of colonies of the aggressive native bird, the noisy miner, the influence of woodland predators on the risk of artificial nest predation was low compared with that of habitat generalist predators. Outside noisy miner colonies, we found significant edge effects with greater predation rates for artificial nests within woodland patches located closer to the agricultural matrix. Furthermore, the density of habitat generalist predators increased with the extent of irrigated land-use, suggesting that in the absence of noisy miner colonies, nest predation increases with land-use intensity at the landscape scale.

Key-words: additive predation model; artificial nest; habitat generalist predator; landscape structure; nest predation.

INTROUDCTION

Within agro-ecosystems globally, many passerine bird populations are in decline (Johnson *et al.* 2011). Nest success is a key driver of population dynamics in these ecosystems (Chalfoun *et al.* 2002a; Johnson 2007; Siriwardena *et al.* 2001), with nest predation the main cause of nest failure for open-nesting passerines (Martin 1992; Ricklefs 1969; Skutch 1966). Numerous studies have suggested that habitat loss and fragmentation lead to an increase in the density of generalist predators and increase the exposure of breeding habitats to these predators, thus increasing the risk of nest predation (Andrén 1992; Bayne and Hobson 1997; Duffy 2003; Ford 2011). However, these studies have failed to reach a consensus on the effects of habitat fragmentation, with the role of factors such as land-use intensity and interspecific competition remaining poorly understood.

Predation rates are often higher where wooded native vegetation abuts agricultural or urban land. In northern America, the abundance of avian nest predators has been shown to increase with the amount of forest edge habitat in fragmented landscapes (Niemuth and Boyce 1997; Nilon *et al.* 1995; Robbins 1980). In western Massachusetts, avian nest predators were more abundant in forest landscapes with greater housing density (Kluza *et al.* 2000). This response may be explained by nutritional subsidies offered by matrix habitats. For example, the presence of suburban development can support very high densities of nest predators such as the blue jay (*Cyanocitta cristata*) (Fretwell 1972) and the raccoon (*Procyon lotor*) (Hoffman and Gottschang 1977).

Understanding the processes influencing nest predation requires testing ecological theory with empirical data to identify potential causal processes (*sensu* Fretwell 1972; Shipley 2000). However, the results of the majority of studies of the effect of edges on nest predation have been ambiguous and somewhat contradictory (Lahti 2001). In addition, empirical landscape-scale studies have failed to reach a consensus on the impacts of landscape change (both landscape composition and configuration) on nest predation (Chalfoun *et al.* 2002b). It is widely hypothesized that increased nest predation in fragmented agricultural landscapes results from higher densities of generalist predators, but most studies do not incorporate potential exacerbating or mediating effects of the landscape matrix (such as acting as a source of generalist predators) into predictive models.

Consideration of the relative influence on nest predation of factors operating at a hierarchy of spatial scales is a potentially promising avenue of inquiry. Patch-scale (1-100s ha) studies can show weak results because of the effects of numerous processes operating at larger spatial scales (Batary and Baldi 2004; Falk *et al.* 2011). In contrast, landscape-scale (1000s ha) studies often omit the contribution of habitat specialist predators and their interactions with generalist predators (Tewksbury *et al.* 2006). Tewksbury et al. (2006) tested the hypothesis that different predators responded to landscape structure at different scales by examining the relative importance of landscape features at multiple spatial scales for different predator groups in western Montana, U.S.A. That study concluded that an Additive Predation Model, which postulates that nest predation is a product of (i) habitat specialists driven by processes at the site and patch scale, and (ii) generalist agricultural predators driven by landscape-scale processes, best predicts the link between landscape structure and nest predation. Predictive models for nest predation, therefore, cannot ignore the complex processes that may be interacting to influence predator density and activity across multiple spatial scales.

In this study, we tested the validity of the Additive Predation Model with a simplified hypothesis: artificial nest predation is primarily influenced by the density of habitat generalist nest predators and the density of woodland nest predators, which are influenced by landscape structure, and site- and patch-level habitat factors, respectively (Fig. 1). We defined habitat generalist nest predators as birds that forage extensively across different habitat types including the agricultural matrix and depredate nests. In contrast, we defined woodland nest predators as birds that are dependent on patches of woodland habitat for the majority of their resource requirements, but also depredate nests. This study considered only avian species as potential nest predators because previous research suggests that birds are the main nest predators in the study area (Zanette and Jenkins 2000).

We tested this hypothesis in a woodland landscape fragmented by mixed cropping-grazing land uses. The study area is located in subtropical eastern Australia. Here, habitat generalist predatory birds, especially corvids, are common across the agricultural matrix, while predatory woodland birds are common within woodland remnants (fragments) and degraded woodland vegetation. The noisy miner (*Manorina melenocephala*) is also abundant within the study area and across eastern Australia (Barret *et al.* 2003). This hyper-aggressive and territorial honeyeater has increased in abundance across its range and appears to benefit from human landscape modification, including habitat loss, habitat fragmentation and habitat degradation (Clarke and Schedvin 1997; Dow 1977; Maron 2009) . The noisy miner is a cooperative-breeder and maintains permanent territories, which are aggressively defended by all colony members against competitors and potential predators (Dow 1977; Clarke and Schedvin 1997). Competitive exclusion of other avian species by the noisy miner is well documented (Arnold 2000; Debus 2008; Grey *et al.* 1998; Howes and Maron 2009; Maron and Kennedy 2007; Piper and Catterall 2003), and this species is now recognized as a strongly interacting despotic species with an important influence on avian assemblages (Mac Nally *et al.* 2012; Maron *et al.* 2011). We therefore expected the noisy miner to have a strong influence on the pattern of nest predation in the study area.

We estimated the probability of nest predation from artificial eggs and identified nest predators to species level using camera traps at artificial nest sites. These data were then analyzed using the path analysis form of structural equation modelling to quantify potential causal interactions and identify important mechanisms influencing artificial nest predation.

METHODS

Study area

The study was conducted in the Border Rivers Catchment Area along the Macintyre River in southern Queensland, Australia (Figure 2). The current extent of native vegetation in the study area is 17%, with 22% of the region used for irrigated cropping, 27% for dryland cropping, and 34% for cattle and sheep pastures. Native woodland ecosystems are highly fragmented with many very small patches (< 5 ha) and few large (> 100 ha) patches resulting in a mean patch size of 22.5 ha (standard error: 1.8 ha); however, some landscapes have retained structural connectivity with a network of riparian woodlands.

The catchment area consists of alluvial plains and riverine landforms with highly fertile, black cracking clay soils. Major vegetation types include *Eucalyptus* open/grassy woodlands and *Casuarina* woodlands, with River Red Gums (*Eucalyptus camaldulensis*, Dehnh, 1832) dominating riparian areas. The region experiences hot, wet summers (Dec-Feb) with a mean maximum temperature of 34.1 °C, a mean minimum temperature of 20.3 °C and mean rainfall of 83.7 mm in January. Winters (Jun-Aug) are cool and relatively dry with a mean maximum temperature of 19.1 °C, a mean minimum temperature of 4.5 °C and a mean rainfall of 34.0 mm in July (Goondiwindi Airport station 041521).

Survey design and study sites

Artificial nest predation and bird density data were collected during the spring (September–November) of 2009. A total of 23 discrete patches of woodland vegetation were selected for the location of sites. Woodland patches ranged in size from 10 to 310 ha with shapes varying from rectangular to irregular polygons. Riparian and linear woodland strips were excluded from site selection. At each site, four artificial nests, each with one artificial egg, were placed along a 200 m transect at suitable nesting sites within 50 m intervals, representing a total of 92 nests. Transects were aligned perpendicular from the patch edge towards the patch centre, with the first nest located at a suitable nesting site between 0 m and 50 m from the patch edge. The artificial nests were exposed for seven days without visitation. For logistical reasons, our exposure period was shorter than the average incubation time of most open-nesting passerines and as a result the daily risk of predation may have been lower compared with natural nests. However, our interest was to compare relative predation rates, rather than document absolute rates. At the end of this period, nests were removed and indications of egg predation were recorded, including egg damage, plus other causes of nesting failure such as nest damage and removal of nesting material.

Artificial nests were made from loose coconut fibre compacted into a mould to create an open-cup nest with dimensions similar to the nest of a hooded robin (*Melanodryas cucullata*), (nest dimensions: exterior: 8.5 x 6.5 cm, interior: 5.6 x 3.5 cm). This species was chosen because it nests in an open-cup shaped nest and is representative of the nest type of many declining woodland bird species in eastern Australia, and experiences high rates of nest predation in fragmented agricultural landscapes (Fitri and Ford 2003).

Artificial eggs were made from modelling plasticine with the dimensions of the average hooded robin egg (20 x 16 mm). We used plasticine eggs because indentation left by predators provide an indication of predator identity. A plaster mould was used to create egg halves and a loop of hessian twine was then placed between the halves before remoulding and applying a glossy varnish. Plasticine was of a bluish-green colour, similar to the colour of some hooded robin eggs (Beruldsen 2003). Gloves were worn during the nest and egg crafting process and eggs were aired for a minimum of 24 hours. Within each transect segment, nests were located in the most suitable location nearest to the transect. Brown hessian twine was used to secure the egg and nest to a horizontal branch or fork of a tree or shrub at approximately 1.2 m above the ground, typical of the nest location of the hooded robin (Higgins and Peter 2002). No attempt was made to conceal the nest, as hooded robins typically nest in highly exposed locations (Beruldsen 2003; Higgins and Peter 2002).

Predators were identified to species level from video recording and still photography. Motion-triggered cameras were placed at each artificial nest. We used the Moultrie GameSpy D40 with a 4.0 megapixel camera and laser trigger, which takes three consecutive colour photos with an automatic flash engaged at night, and the Primos TruthCam 46 5.0 megapixel camera with a passive infrared motion sensor and infrared light-emitting diodes which records 30 seconds of colour video by day and black and white Infra-Red video by night. Media files were automatically saved to a Secure Digital card. Egg indentations were also used as an indicator of predator identity. We staggered the deployment of artificial nests and camera traps to sites at a rate of one site per day using a total of 28 camera traps.

Avian predator and noisy miner density surveys

For each study site, the density of all diurnal birds, excluding aquatic and semi-aquatic species, were recorded by sight and sound within a 2 ha (400 x 50 m) survey area centred on the patch centroid for 20 minutes using the active search method. This method allowed the observer to track cryptic species within the search area to make certain of identification. Counts of birds during a specified time period provided an index of density (Bibby *et al.* 2000). Three repeat surveys were conducted for each site on non-consecutive days during the artificial nest exposure period, with the density index calculated from the mean number of individuals of the three repeats. Sites with exposed artificial nests were surveyed in random order. Birds above the canopy were not recorded with the exception of aerial insectivores, predators and scavengers. Surveys were conducted up to 4 hours after sunrise and 2 hours before sunset. All surveys were conducted by the same observer (O.R.).

Survey sites were located in the centre of woodland patches, and not along artificial nest transect sites, which began at the patch edge. Individuals that do not penetrate the patch edge cannot influence the probability of predation for nests further within woodland patches, and counts of predators on the patch edge may inflate perceived predation risk for these nests.

Habitat generalist species such as the Torresian crow (*Corvus orru*) and the Australian magpie (*Cracticus tibicen*) were recorded in the study area well within woodland habitat and observed depredating artificial nests within woodland patches more than 100 m from the patch edge, although their density may have been higher closer to the patch edge.

Most survey areas were intersected by a nest transect. However, 9 bird survey sites were located more than 200 m from the patch edge, which was also the maximum distance between artificial nests and the patch edge. Within these patches, the survey sites were separated from the nest transect by distances ranging 25-530 m. This may not be a significant caveat, with a study in remnant box-ironbark forest in central Victoria, Australia, concluding that woodland-dependent birds occurred at similar densities throughout 2000 ha woodland patches (Harwood and Mac Nally 2005). Previous studies have surveyed predator activity around nests at different times to the exposure of nests (Major *et al.* 1999), while other studies have surveyed predator activity at random locations throughout the patch without reference to the relative location of artificial nests (Gardner 1998). We chose to survey potential predators and the noisy miner during the exposure period in an adjacent location to minimise investigator disturbance. Because nest transects and survey sites were perpendicular to each other, overlap between intersecting sites was minimal, and the observer was careful not to disturb the nest trees during surveys.

Explanatory variables

Potential environmental drivers were recorded at four spatial scales: nest-scale, site-scale, patch-scale and landscape-scale (Table 1). Nest-scale variables varied for each individual artificial nest and were grouped at the site level. At the nest-scale, we included the distance in metres between each artificial nest and the closest edge of the woodland patch.

At the site-scale (2 ha), we included the density of noisy miners (*Manorina. melanocephala*), a communally breeding native honeyeater, as potential competitors of predators because of the strong influence of this species on the composition of avian assemblages (Howes and Maron 2009; Lindenmayer *et al.* 2010; Maron *et al.* 2011) and its aggressive territorial behaviour directed towards potential competitors and nest predators (Maron 2009).

We also included the presence or absence of a noisy miner colony as a two-level factor, where colonized sites had an average density of noisy miners of >2.5 individuals per site and absence was ≤2.5 individuals per site. We chose 2.5 as the cut-off for colony presence because noisy miner colonies by definition contain more than two individuals, with several males helping to feed the offspring of a single female (Dow 1979). Colonies of noisy miners can number several hundred birds which unite to mob predators from the colony area (Dow 1979). Therefore sites with an average density of miners >0 and ≤2.5 are unlikely to be within colony's territory but may be occasionally used for dispersal or extra-territorial foraging forays.

We calculated the average density of grey butcherbirds (*Cracticus torquatus*), apostlebirds (*Struthidea cinerea*), grey-crowned babblers (*Pomatostomus temporalis*), and grey shrike-thrushes (*Colluricincla harmonica*) as an index of woodland nest predator density. These species were defined *a priori* as woodland species because of their classification as woodland-dependent species. An index of habitat generalist nest predator density was also calculated from the average density of Australian ravens (*Corvus coronoides*), Torresian crows, Australian magpies, and pied butcherbirds (*Cracticus nigrogularis*). These species were defined *a priori* as habitat generalist species because of their classification as either open-tolerant or open-country species. Each of these species, including both woodland species and habitat generalists, were classified as nest predators after being identified depredating artificial nests by camera traps, as well as being identified as nest predators from historical records (Higgins *et al.* 2006; Higgins and Peter 2002). The Australian magpie and the Australian raven were included in the index of habitat generalist predators despite being recorded by camera traps only once depredating artificial nests, because the dietary records for these species strongly suggest they are significant predators of eggs and nestlings.

We mapped the extent and configuration of woodland habitat and irrigated land-use within 1 km radius landscapes surrounding the mid-point of the nest transect, from Spot-5 multi-spectral satellite imagery (spatial resolution 5 m) using ArcMap, using ArcGIS version 9.3. Woodland habitat was defined as native vegetation with a minimum of five trees per hectare so as to delineate habitat patches from crops we ignored patches smaller than 0.0025 ha. We included all woodland vegetation types as woodland habitats. We analysed a shape file of habitat and irrigation polygons with Patch Analyst version 9.5 (Kaukinen *et al.* 2008) and calculated the extent of woodland habitat, the number of woodland patches and the extent of irrigated land-use. We chose a 1 km radius landscapes to replicate the scale used by Tewksbury et al. (2006). We quantified patterns of habitat loss and fragmentation at the patch-scale (10–310 ha) with patch size and corrected perimeter area ratio (CPA), and at the landscape-scale (314 ha) with woodland extent and number of woodland patches within 1 km of the nest transect. CPA is a measure of patch shape complexity that varies independently of patch size (Kluza *et al. 2000*).We limited the analysis to a single fragmentation index because of the high degree of correlation between many measures of habitat configuration (Fahrig 2003; Turner *et al.* 2001).

Statistical analysis

We modelled the probability of artificial nest predation at the nest-level (n=92) in a multivariate setting to include interactions between environmental and biological explanatory variables. We used structural equation modelling in the Statistica 9 program (StatSoft 2009) to analyze correlations between variables and test the predictions. This technique has been widely used in the social sciences (Anderson and Gerbing 1988) and utilizes path analysis theory to describe the probability distributions generated by the relationships between potential causal processes (Shipley 2000). This method has rarely been used to quantify causal interactions between landscape patterns and predation risk, although it has been used to identify the effect of landscape structure on glider species abundance (McAlpine and Eyre 2002). This method has an advantage over other modelling techniques as it is based on path analysis theory, which specifies the direction of causality between variables, as opposed to a simple statistical correlation which specifies an asymmetrical relationship with an unresolved causal structure (Shipley 2000).

Structural equation modelling implies a specific covariance structure among variables. For example, if the joint probability density of X and Y is the product of the probability density of X and the probability density of Y they are unconditionally independent:

$$\text{If } I(X,\varphi,Y) \text{ then } P(X,Y) = P(X) \text{ x } P(Y)$$

In addition, X and Y are conditionally independent on another set of variables Z, if the joint probability density of X and Y given Z equals the product of the probability density of X given Z and the probability density of Y given Z for all values of X, Y and Z for which the probability density of Z is not equal to zero:

$$\text{If } I(X, Z,Y) \text{ then } P(X,Y|Z) = P(X|Z) \times P(Y|Z)$$

We can then compare the observed pattern of covariance between variables because of their joint probability distributions with the pattern of covariance predicted by the hypothesized structural equation. Because of the hierarchically structured nature of our data, we fitted a multi-level structural equation model to account for the non-independence of nests within sites/landscapes. In order to fit a multi-level model in the Statistica program, we created a multi-group model with two levels. For the covariance structure of the first level (nest level), we specified a within-site causal structure. We then created a between-sites covariance matrix for level 2 (site/patch/landscape-scales) and specified both a within-site causal structure and a between-site causal structure. The two causal structures are linked by latent variables that represent the true values of the group means in the statistical population (Shipley 2000).

Because many of the explanatory variables were non-normal because of the skewed nature of the count data, we used Asymptotically Distribution Free (Gramian) (ADFG) statistical estimation in the modelling process, which allows the analysis of non-normal data without losing the chi-squared distribution of the test statistic (Steiger 1995). We analyzed standardized correlation matrices to conduct completely standardized path analysis and correctly estimate standard errors. We used an ADFG discrepancy function with preliminary Generalized Least Squares estimation, fixed manifest exogenous variables and a cubic interpolation line search method to run the model in the STATISTICA program.

Because noisy miners are aggressively territorial and exclude smaller birds from the territory area, small woodland-dependent passerines are unlikely to nest within noisy miner territories. We therefore also conducted the analysis with a subset of the data, excluding data from nests within noisy miner colonies (> 2.5 individuals/site) leaving 36 nests from sites outside noisy miner colonies. Within this data subset, noisy miners were detected at two sites (8 nests) with a maximum average density of 0.33 per site.

RESULTS

The total percentage of artificial nests that were depredated was 76.1% (Table 2). From markings on artificial eggs, we recorded 49 bird predation events. We were unable to differentiate between woodland predators and habitat generalist predators from markings. Twenty eggs were removed from the nest and lost, leaving predator identity unknown. On many occasions, the camera traps failed to record evidence of nest predation. For example, 23 predation events attributed to birds from egg indentations were unrecorded by camera traps. Apostlebirds were recorded most often depredating artificial nests by camera traps with eight predation events (Table 3). Recordings of predation by mammals were rare, with three mammalian predation events recorded, although only one of these eggs was recovered. Reptiles were infrequently recorded near artificial nests, and not recorded depredating nests.

The best structural equation model for all nests (including those within noisy miner colonies) based on AGFI included five explanatory variables at the site, patch and landscape scales (d.f: 12, ADFG chi-squared: 156.69, p-value: <0.001, AGFI: 0.99) (Fig. 3). With the exception of the woodland predator density, the statistical significance of all explanatory variables and the overall model was very high (P<0.001). This model did not support the structure of the Additive Predation Model. Corrected perimeter-area ratio had the largest effect on artificial nest predation with a greater probability of nest predation within more irregularly shaped patches (Fig 4). Noisy miner colony presence had a smaller negative effect on artificial nest predation. Noisy miner colonies had a strong positive effect on woodland predator density, which had no direct effect on artificial nest predation. The average density of noisy miners increased with the extent of irrigated cropping. Habitat generalist predator density was not included in the best model based on AGFI. The extent of woodland habitat and the number of woodland patches was also excluded from the model based on AGFI.

The analysis of the data subset, excluding nests within noisy miner colonies, produced different results. The best structural equation based on AGFI included five explanatory variables at the nest, site, patch and landscape scales (df: 12, ADFG chi-squared: 58.24, *P*-value: <0.001, AGFI: 0.92) (Fig. 5). This model also did not support the Additive Predation Model, with a non-significant influence of woodland predator density on the probability of nest predation. Distance from the patch edge had the largest direct effect on the probability of artificial nest predation, with a negative influence (Fig 6). The effect of the average density of habitat generalist predators was also large, with a positive influence on predation. The extent of irrigated land-use had the largest standardized effect, with a positive influence on the density of habitat generalist predators. Inclusion of the variables patch shape complexity, noisy miner density and noisy miner colony did not improve the AGFI of this model.

DISCUSSION

We found that the predation of artificial nests is influenced by patterns and processes occurring at multiple spatial scales. Despite this, we found little support for the Additive Predation Model through the correlation structure of the data, with no significant influence of woodland predator density on the probability of nest predation, and habitat generalist predators only important in the absence of noisy miner colonies. The presence of noisy miner colonies appears to disrupt ecological processes important for nest predation, such that the Additive Predation Model is not supported.

Artificial nests inside and outside noisy miner colonies

We found no significant relationship between the density of nest predators and the probability of artificial nest predation and therefore, no support for the Additive Predation Model. In contrast, noisy miners had a significant positive influence on the density of woodland predators, although they also reduced the probability of artificial nest predation. The positive influence of noisy miner colonies on woodland predator density may be explained by a territorial or nesting association between the noisy miner and the grey butcherbird. Some studies have suggested a potential association between the grey butcherbird and *Manorina* species (Fulton 2008; Maron 2009). Although the grey butcherbird is itself a nest predator, it is primarily insectivorous and while noisy miners may benefit from the butcherbird's assistance in repelling larger nest predators, the grey butcherbird may benefit from the exclusion of other insectivores (Fulton 2008), as well as a decreased risk of nest predation within noisy miner colonies. Several studies have documented bird species exploiting the nest predator defence behaviour of 'protective' species, including other birds (Quinn and Ueta 2008). Noisy miners are aggressively territorial all year round, with individuals cooperating to defend the colony from nest predators and competitors (Dow 1979). In southern Queensland, this species has been observed in aggressive interactions with a nest predator, the pied currawong (*Strepera graculina*), more frequently than would be expected on the basis of the incidence of that species (Maron 2009).

The noisy miner appears to disrupt the effect of both woodland and habitat generalist predators on nest predation rates with a negative influence on the risk of nest predation, and this result provides further support for a potential benefit to butcherbirds of nesting within noisy miner colonies. Furthermore, we suggest that the ‘protective’ effect of noisy miner colonies is such, that in landscapes where noisy miners occur, the Additive Predation Model does not apply. The aggressive territorial behaviour of the noisy miner may influence ecological processes important for nest predation through the behavioural ecology of nest predators. Persistent and cooperative mobbing behaviour from colony members may dissuade nest predators from foraging within noisy miner colonies, or nest predators may reduce their search effort in response to an expected low density of active passerine nests within noisy miner colonies.

This counterintuitive result of less nest predation where there are more woodland predators may also be explained by the low importance of smaller woodland predators in the study area. Thus, habitat generalist predators may have been responsible for nest predation, even though their density did not correlate with the probability of nest predation, because of interference from the noisy miner.

The positive influence of patch shape complexity on nest predation indicates that edge effects may influence the probability of nest predation (Gardner 1998). More irregularly shaped patches have a greater proportion of edge habitat relative to area, and nests within these patches suffer greater exposure to the production matrix (Dunford and Freemark 2005; Saunders and De Rebeira 1991; Sisk *et al.* 1997). In this study, patches with the lowest shape complexity were close to rectangular, while patches with the highest shape complexity were irregular in shape with few straight edges (Fig. 7). Predators, such as habitat generalist avian species within the production matrix, may make forays from the patch edge into woodland habitat to depredate nests (*sensu* Andrén 1992).

Artificial nests outside noisy miner colonies

Outside noisy miner territories, we found little support for the Additive Predation Model. Woodland and habitat generalist predators responded to the patch and landscape scales respectively, as predicted by the conceptual model, but the influence of woodland predator density was not statistically significant. The relatively large and positive influence of distance to patch edge indicates that the probability of predation is greater for nests closer to the patch edge, and is supported by previous studies in similar landscapes (Gardner 1998; Piper and Catterall 2004). This edge-effect suggests that generalist predators associated with the matrix or the woodland patch edge, known as 'matrix invaders' (sensu Major *et al.* 1999), are moving short distances from the patch edge into woodland habitat (<200 m) to depredate nests.

In our model, habitat generalist predators had a large effect on artificial nest predation, compared with a relatively small effect of woodland predators. The low importance of woodland predator density suggests that these species are relatively infrequent nest predators in the study area, as woodland predators occurred in greater density than habitat generalist predators. It should also be noted that the importance of habitat generalist predators relative to woodland predators was not reflected in the records of the camera traps, where 16 predation events were attributed to woodland predators and only 9 predation events attributable to habitat generalists (Table 3). However, as the instigators of another 41 predation events were not recorded, it is difficult to draw conclusions from the camera trap data. In addition, the relative importance of different predator groups, determined from artificial nests, should be interpreted with caution, as real nests in the study area may be predated by different predators in different proportions (Part and Wretenberg 2002).

Matrix effects

In comparison to woodland predators, habitat generalist predators had a large positive influence on the probability of nest predation. Habitat generalist predators responded to variation in the matrix at the landscape scale, suggesting that nest predation can be influenced by landscape scale patterns of land use (Dunford and Freemark 2005). Our finding of a positive influence of irrigated land use on the density of habitat generalist predators points to a potential mechanism through which increasing land use intensity could affect woodland bird communities (Bennett and Ford 1997). The extent of irrigated cropping was not correlated with the extent of the agricultural matrix or woodland habitat. The extent of irrigated cropping therefore reflects the intensity of land-use within the production matrix, independent of habitat loss or fragmentation.

The importance of land-use intensity for nesting success of birds has not been previously tested, except for a single study investigating the nest success of skylarks (*Alauda arvensis*) in southern England (Wilson *et al.* 1997). The authors concluded that the breeding success of this species was greater on organic farms than on intensively managed farms. In Australian agricultural landscapes, species including the Australian magpie, pied butcherbird and Australian raven use woodland habitat primarily for roosting and breeding, while deriving extra foraging opportunities from the matrix (Lynch and Saunders 1991; Saunders and Ingram 1995). High intensity irrigated cropping, as opposed to broad-acre dryland cropping or pasture, may provide high quality foraging habitat for habitat generalist predators, and when adjacent to woodland habitat, habitat generalist predators may benefit from resource complementation (Dunning *et al.* 1992). Increasing land-use intensity across the agricultural landscapes of eastern Australia may provide a greater availability of resources such as prey for habitat generalist predators, allowing them to inhabit woodland remnants in greater densities with adverse impacts on open-nesting woodland passerines (Major *et al.* 1996).

Approach and limitations

The main caveat of the study is the use of artificial nests. Opinion is divided over their use and some authors maintain that artificial nests poorly reflect natural processes (Major 2000; Zanette 2002). Whilst not ideal for quantifying absolute nest success, artificial nests can be used to compare relative predation rates between treatments (Batary and Baldi 2005; Gotmark *et al.* 1990; Major *et al.* 1994; Roos 2002). In contrast to artificial nests, nest predation at real nests may be confounded by species-specific parent behaviour and investigator disturbance at real nests may bias predation rates (Gotmark 1992; Major 1990).

Conclusion

We conclude that the Additive Predation Model is not applicable to ecological processes important for nest predation in agricultural regions of eastern Australia, potentially because of the influence of the noisy miner. Our results suggest that the noisy miner influences ecological processes that are important for nest predation through aggressive, territorial behaviour. The density of woodland predators within woodland patches had little impact on the probability of artificial nest predation. Edge effects and the density of habitat generalist predators had the greatest influence on the probability of artificial nest predation. Habitat fragmentation at the landscape scale was not important but land-use intensity at that scale was important and positively influenced the density of habitat generalist nest predators within woodland patches.

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Table 1. Summary of explanatory variables included in structural equation modelling as potential predictors of the probability of artificial nest predation.

Scale	Variable	Description
Landscape	*Woodland extent*	The total extent (ha) of woodland vegetation within the surrounding landscape (1 km radius surrounding the mid-point of the nest transect), mean: 101.09, range: 10-180.
	Irrigation extent	The total extent (ha) of irrigated land use within the surrounding landscape (1 km radius surrounding the mid-point of the nest transect), including all irrigated crop types, fallow fields, channels and reservoirs, mean: 57.65, range: 0-205.
	Subdivision	The total number of discrete patches of woodland vegetation within the surrounding landscape (1 km radius surrounding the mid-point of the nest transect), mean: 5.09, range: 1-12.
Patch	*Patch size*	The total area of the woodland patch (ha) surrounding each survey site, mean: 70.35, range: 10-310.
	Corrected perimeter to area ratio	The corrected perimeter to area ratio (CPA) is a measure of patch shape complexity and is calculated by dividing the perimeter of the study woodland patch by the square root of the product of 4π and the area of the patch. This correction results in a ratio of 1:1 for circular patches, and lager values for skinny or irregular patches, mean: 149.91, range: 84-278.
Site	*Habitat generalist predators*	The average density of avian habitat generalist nest predators including the Torresian crow, Australian Raven, Australian magpie and pied butcherbird at the study site during the nest exposure period, mean: 0.94, range: 0-4.67.
	Woodland predators	The average density of avian woodland nest predators including the grey butcherbird, apostlebird, grey-crowned babbler and grey shrike-thrush at the study site during the nest exposure period, mean: 2.82, range: 0-9.33.

	Noisy miner density	The average density of noisy miners at the study site during the nest exposure period. This native passerine is an aggressive colonial species, mean: 3.65, range: 0-10.67.
	Colony	Presence or absence of a noisy miner colony, sites colonized when average noisy miner density above 2.5, mean: 0.61, range: 0-1.
Nest	*Distance*	The horizontal distance (m) from the artificial nest to the closest edge of the woodland patch, mean: 97.65, range: 0-197.

Table 2. Summary statistics from the artificial nests and decoy plasticine eggs. Failure rate includes failures due to predation and nest damage. Predator type was determined from markings left on artificial eggs.

Sites	23
N (nests)	92
Failure rate (%)	77.2
Egg predation rate (%)	76.1
Egg predation rate (%) of nests outside noisy miner colonies	83.3
Nest damage rate (%)	39.8
# predations by birds	49
# predations by mammals	1
# predations by reptiles	0
# predations by unknown	20

Table 3. Count of predation events for each species of nest predator identified by camera traps at artificial nest sites. Predation events counted when still photography or video recording show predators damaging or removing the egg.

Common name	**Species name**	**Count**
Apostlebird	*Struthidea cinerea*	8
Grey butcherbird	*Cracticus torquatus*	5
Torresian crow	*Corvus orru*	4
Pied butcherbird	*Cracticus nigrogularis*	3
Grey-crowned babbler	*Pomatostomus temporalis*	2
Australian magpie	*Cracticus tibicen*	1
Grey shrike-thrush	*Colluricincla harmonica*	1
Australian raven	*Corvus coronoides*	1
White-winged chough	*Corcorax melanorhamphos*	1
Common brushtailed possum	*Trichosurus vulpecula*	1
Brush-tailed phascogale	*Phascogale tapoatafa*	1
Rodent	*Order Rodentia, unknown sp.*	1

Fig. 1. Schematic diagram of the hypothesis to be tested with artificial nests, simplified from the Additive Predation Model (Tewksbury *et al.* 2006). Avian habitat generalist predators include the Torresian crow, Australian raven, Australian magpie and pied butcherbird, which are defined as open-country species that range extensively across the agricultural matrix. Avian woodland predators include the grey butcherbird, the apostlebird and the grey-crowned babbler, which are woodland-dependent and forage predominately within woodland patches.

Fig. 2. Location of the study region and study landscapes (1 km radius circles) surrounding artificial nest sites in southern Queensland (grey shading represents tree cover), and histogram showing the variation in landscape-level woody vegetation cover within the 23 study landscapes.

Fig. 3. Path diagram of the best structural equation model for the probability of predation on artificial nests based on Adjusted-Goodness-of-Fit Index (AGFI) (n: 92, df: 12, Asymptotically Distribution Free (Gramian) Chi Square: 156.69, AGFI: 0.99, p-value: <0.001). Standardized parameter estimates and standard errors displayed within boxes. Parameters marked '***' are statistically significant with an α-level of 0.001. Arrow width represents relative effect size. Solid arrows are positive, dashed arrows are negative. Latent errors for exogenous variables are not shown.

Fig. 4. Predicted values for the probability of artificial nest predation (black line) plotted against corrected perimeter ratio (CPA) showing a 95% confidence interval (grey shading).

Fig. 5. Path diagram of the best structural equation model for the probability of predation on artificial nests using a subset of the samples excluding nests within noisy miner colonies (noisy miner density > 2.5/site) based on Adjusted-Goodness-of-Fit Index (AGFI) (n: 36, df: 12, Asymptotically Distribution Free (Gramian) Chi Square: 58.24, AGFI: 0.92, p-value: <0.001). Standardized parameter estimates and standard errors displayed within boxes. Parameters marked '***' are statistically significant with an α-level of 0.001 . Arrow width represents

relative effect size. Solid arrows are positive, dashed arrows are negative. Latent errors for exogenous variables are not shown.

Fig. 6. Predicted values for the probability of artificial nest predation (black line), in the absence of noisy miner colonies, plotted distance to the patch edge (m) showing a 95% confidence interval (grey shading).

Fig. 7. Schematic diagram of (A) a woodland patch (black) with low shape complexity within a 1 km radius landscape (open black circle) composed of irrigated land-use (grey) and other land uses (white) with low exposure to predators (arrows) in the production matrix, and (B) a woodland patch (black) with high shape complexity and relatively high exposure to predators (arrows) in the production matrix associated with a greater proportion of edge habitat adjacent to the production matrix (grey and white).

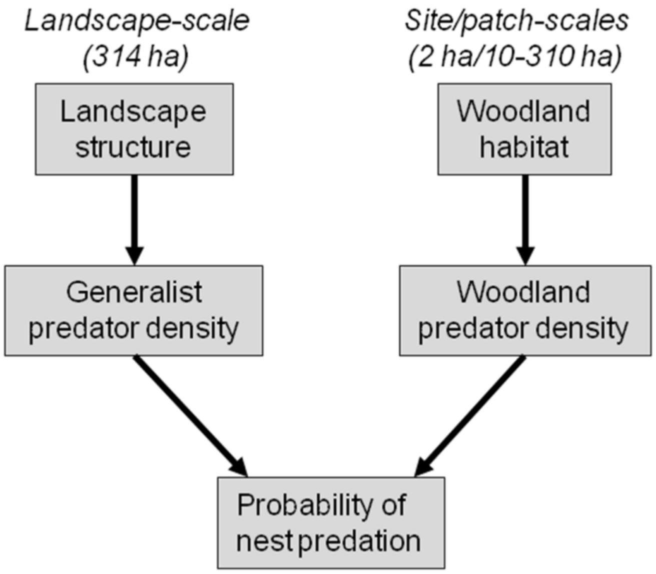
Landscape-scale
(314 ha)
Site/patch-scales
(2 ha/10-310 ha)
Landscape structure
Woodland habitat
Generalist predator density
Woodland predator density
Probability of nest predation

Fig. 1.

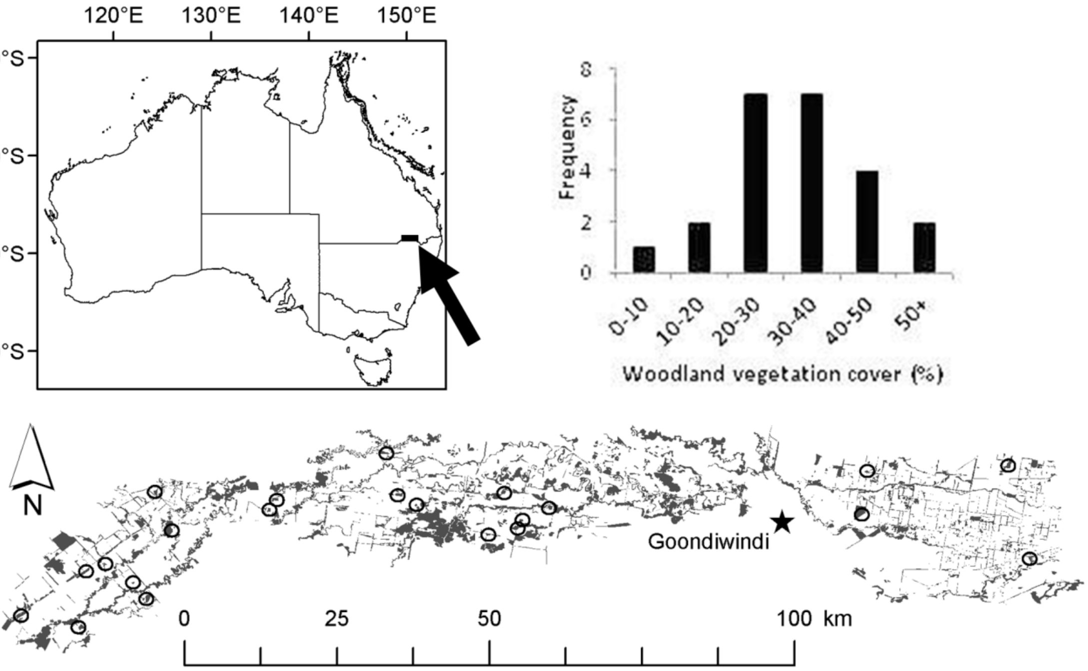
120°E
130°E
140°E
150°E
10°S
20°S
30°S
40°S
Frequency
8
6
4
2
0
0-10
10-20
20-30
30-40
40-50
50+
Woodland vegetation cover (%)
N
Goondiwindi
0
25
50
100 km

Fig. 2.

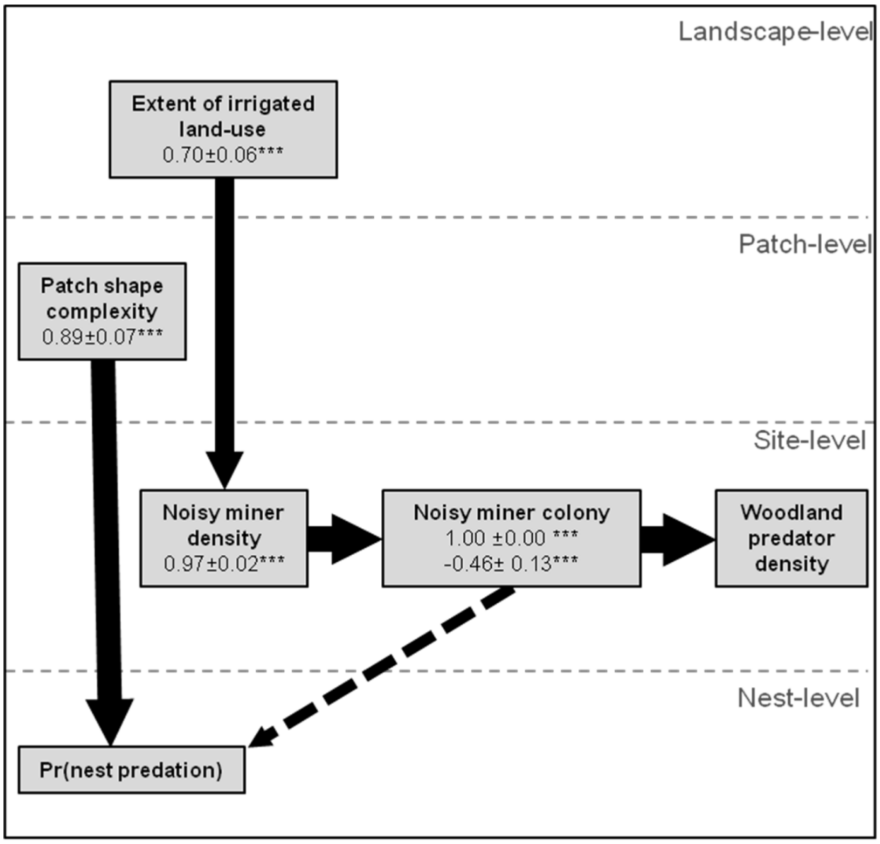
Landscape-level
Extent of irrigated land-use
0.70±0.06***
Patch-level
Patch shape complexity
0.89±0.07***
Site-level
Noisy miner density
0.97±0.02***
Noisy miner colony
1.00 ±0.00 ***
-0.46± 0.13***
Woodland predator density
Nest-level
Pr(nest predation)

Fig. 3.

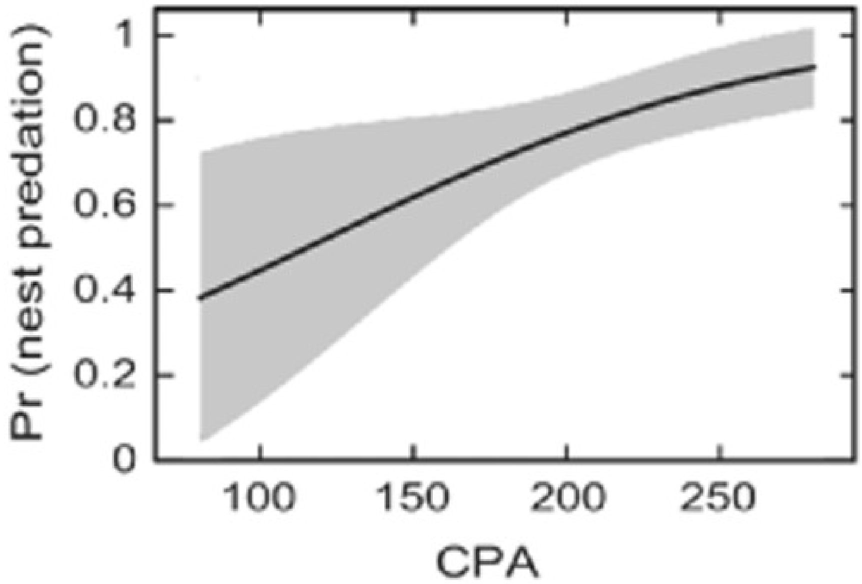

Fig. 4

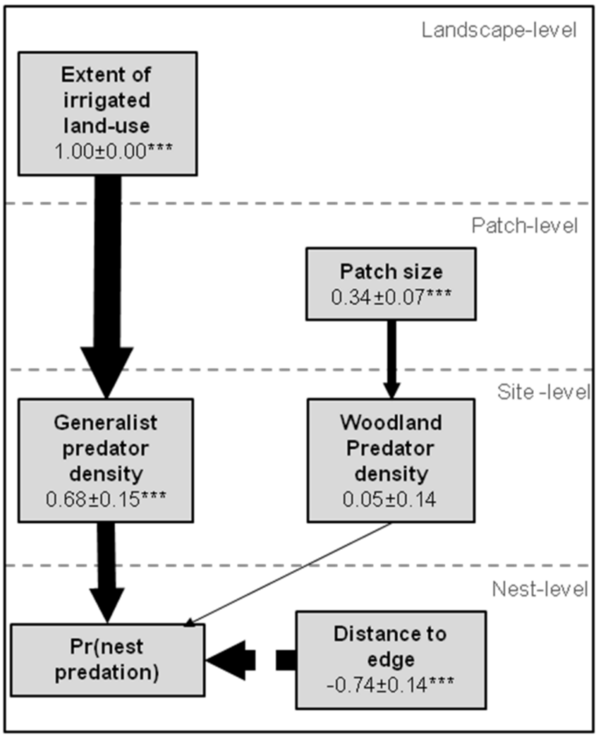
Landscape-level
Extent of irrigated land-use
1.00±0.00***
Patch-level
Patch size
0.34±0.07***
Site -level
Generalist predator density
0.68±0.15***
Woodland Predator density
0.05±0.14
Nest-level
Pr(nest predation)
Distance to edge
-0.74±0.14***

Fig. 5.

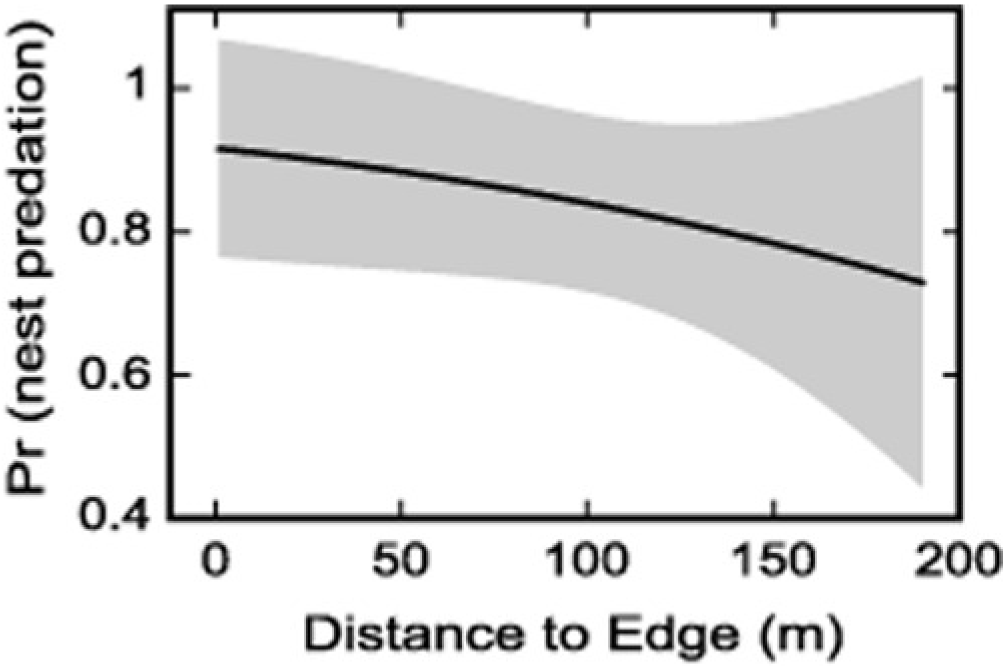

Fig.6

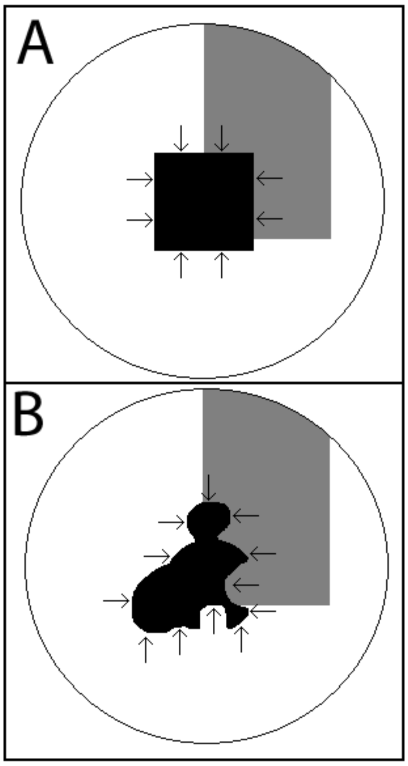

Fig. 7