Effects of entrance size, tree size and landscape context on nest box occupancy: Considerations for management and biodiversity offsets

Darren S. Le Roux [a,*], Karen Ikin [a], David B. Lindenmayer [a], Gideon Bistricer [b], Adrian D. Manning [a], Philip Gibbons [a]

[a] The Fenner School of Environment and Society, The Australian National University, Canberra 0200, Australian Capital Territory, Australia
[b] Institute of Natural and Mathematical Sciences, Massey University, Palmerston North 4474, New Zealand

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ABSTRACT

The effectiveness of nest boxes as a management and biodiversity offset tool remains equivocal and controversial. Improving nest box programs requires urgent empirical research to identify the spatial factors that affect occupancy outcomes. Understanding which fine, local and landscape-level attributes influence nest box selection by wildlife can assist practitioners in refining nest box designs and placement in the field. We asked: Does entrance size, tree size and landscape context affect nest box occupancy? We monitored 144 nest boxes with six different entrance sizes (20, 35, 55, 75, 95 and 115 mm diameter), secured to individual trees of three sizes (small 20–50 cm DBH, medium 51–80 cm and large >80 cm) situated in four different landscape contexts with varying degrees of modification (reserves, pasture, urban parklands and urban built-up areas). We found that six common native and exotic species accounted for 89% of nest box occupancies. Entrance size had a significant effect on overall occupancy. Nest boxes with larger entrance sizes (115, 95, 75 and 55 mm) were occupied more ($\geqslant$77% of nest boxes occupied) than nest boxes with smaller entrance sizes (35 and 20 mm; $\leqslant$45% of nest boxes occupied). Tree size and landscape context had no significant effect on overall occupancy. However, multinomial analysis revealed that entrance size and landscape context affected occupancy by common fauna (i.e. species that occupied $\geqslant$5% of nest boxes). Nest boxes with small (20 and 35 mm), intermediate (55 and 75 mm) and large (95 and 115 mm) entrance sizes were predominately occupied by the European honey bee *Apis mellifera*, common exotic (e.g. common myna *Acridotheres tristis*) and native birds (e.g. eastern rosella *Platycercus eximius*), and the common brushtail possum *Trichosurus vulpecula*, respectively. Nest boxes in reserves and pasture had near equal occupancy by common fauna while nest boxes in urban parklands and urban built-up areas were predominately occupied by the common brushtail possum and the European honey bee. Establishing nest boxes with different entrance sizes could maximise occupancy by a variety of common hollow-nesting species. Targeting occupancy by some species requires consideration of landscape context but not tree size. Nest boxes were predominately occupied by a few common native and exotic species, suggesting that nest boxes may not be highly effective management and biodiversity offset tools for rare and threatened taxa in modified landscapes. Management policies and practices aimed at avoiding the loss of large, hollow-bearing trees must be prioritised.

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1. Introduction

Tree hollows (or cavities) are a critical habitat resource for fauna globally (Gibbons and Lindenmayer, 2002; Cockle et al., 2011). Hollows provide shelter and breeding opportunities for mammals (Lindenmayer et al., 1990), birds (Newton, 1994), reptiles (Webb and Shine, 1997), and invertebrates (Ranius, 2002). In modified landscapes worldwide (e.g. agricultural land, production forests and urban environments), human activities, such as land clearance, logging and managed tree removal, have facilitated the decline of large, hollow-bearing trees (Gibbons et al., 2010; Lindenmayer et al., 2012; Le Roux et al., 2014b; McIntyre et al., 2015). Reduced availability of hollow-bearing trees can have serious conservation implications for hollow-using fauna, especially for obligate hollow-nesters that may face population bottlenecks

* Corresponding author.
E-mail addresses: darren.leroux@anu.edu.au (D.S. Le Roux), Karen.Ikin@anu.edu.au (K. Ikin), David.Lindenmayer@anu.edu.au (D.B. Lindenmayer), g.bistricer@gmail.com (G. Bistricer), Adrian.Manning@anu.edu.au (A.D. Manning), Philip.Gibbons@anu.edu.au (P. Gibbons).

and extinction (Cockle et al., 2010; Manning et al., 2012). Time lags associated with hollow formation mean that some management strategies aimed at arresting hollow decline (e.g. increasing tree recruitment) will be unable to alleviate short-term deficits in hollow availability (Gibbons et al., 2008; Manning et al., 2012; Le Roux et al., 2014b). Nest boxes offer an alternative management strategy that bypasses the time needed for hollows to form naturally, potentially providing immediate benefits for hollow-using species (Lindenmayer et al., 2009; Berthier et al., 2012).

In some cases, the recovery of hollow-nesting animal populations has partly been attributed to nest box additions (e.g. southern flying squirrels *Glaucomys volans* in logged plantations; Taulman et al., 1998; see also Goldingay et al., 2015). However, in many other cases, the efficacy of nest box programs remains questionable and controversial because of low occupancy rates and exploitation by non-target fauna (Grarock et al., 2013; Priol et al., 2014). A further limitation of nest box programs is the rapid rate of nest box attrition due to damage and decay of materials. Lindenmayer et al. (2009) found that most nest boxes had decayed and fallen from trees within ten years limiting long-term effectiveness for the critically endangered Leadbeater's possum *Gymnobelideus leadbeateri*. In contrast, natural hollows likely persist over much longer time periods (Gibbons et al., 2000; Ranius et al., 2009; Lindenmayer et al., 2015). A further limitation for practitioners is the high financial costs that may be associated with nest box construction, monitoring and maintenance (McKenney and Lindenmayer, 1994). These studies highlight that nest box programs supplementing natural hollows over large areas, long time periods, and for threatened species, can be exceptionally challenging to implement.

Despite the limitations outlined above, nest boxes are increasingly being employed as an engineering 'solution' to compensate for the loss of large, hollow-bearing trees removed due to human activities (e.g. Goldingay and Stevens, 2009; Roads and Traffic Authority, 2011; Peste et al., 2015). However, before nest boxes can be used effectively as a management and biodiversity offset tool, it is imperative to first identify ways of improving nest box design and placement in the field. Goldingay et al. (2015) recently highlighted that refinements to nest box design could limit nest box use by pest fauna and improve nest box occupancy by some threatened species over a 10 year period. Previous research studies, predominantly undertaken in Europe and North America, have found that nest box selection by fauna (mostly birds) can be affected in complex ways by a variety of fine, local, and landscape-level attributes (e.g. Herlugson, 1981; Finch, 1989; Blem and Blem, 1991; Bortolotti, 1994; Bolton et al., 2004; Ardia et al., 2006; Smith et al., 2007; Lambrechts et al., 2010; Björklund et al., 2013). By comparison, fewer Australian studies have empirically tested whether species show a preference for specific nest box designs and placement (e.g. Menkhorst, 1984; Smith and Agnew, 2002; Harper et al., 2005; Goldingay et al., 2007, 2015; Durant et al., 2009; Lindenmayer et al., 2009, 2015; Rueegger et al., 2013). More studies are still urgently needed to investigate nest box selection by fauna and, in doing so, also evaluate whether nest box programs can effectively achieve applied conservation objectives.

In this study, we asked: Does entrance size, tree size, and landscape context affect nest box occupancy? These spatial factors were investigated because they can be relatively easily manipulated at the construction and installation phase of nest box programs to potentially influence on-the-ground occupancy outcomes. We tested five predictions (see Table 1): (1) nest boxes with larger entrance sizes will be occupied more than nest boxes with smaller entrance sizes; (2) nest boxes with larger and smaller entrance sizes will be occupied by proportionally larger and smaller-bodied animals, respectively; (3) nest boxes secured to small and medium sized trees, which support fewer natural hollows, will be occupied more than nest boxes secured to large trees, which support more natural hollows; (4) nest boxes placed in modified landscapes, which support fewer hollow-bearing trees, will be occupied more than nest boxes placed in a semi-natural landscape, which supports more hollow-bearing trees; and (5) common adaptable native and exotic species will occupy more nest boxes placed in modified landscapes than nest boxes placed in a semi-natural landscape.

2. Materials and methods

2.1. Study area

We conducted our study in Canberra, Australian Capital Territory (ACT), southeastern Australia. Canberra (covering an area of approximately 810 km^2) is located in a fragmented landscape comprising: urban areas supporting 375,000 people; agricultural land for livestock grazing; and 34 nature reserves managed for conservation (ACT Government, 2011). Land clearance for farming and

Table 1
A summary of study predictions and ecological justifications underpinning these.

Factor	Prediction	Ecological justification
Entrance size	(i) Nest boxes with larger entrance sizes will be occupied more than nest boxes with smaller entrance sizes	Small hollows tend to be naturally more abundant than large hollows and may thus be in less demand by fauna (e.g. Gibbons et al., 2002; Le Roux et al., 2014a). Larger hollows are also likely to be accessed by more species than smaller hollows (e.g. Gibbons and Lindenmayer, 2002)
Entrance size	(ii) Nest boxes with larger and smaller entrance sizes will be preferentially occupied by large and small-bodied animals, respectively	Animals tend to occupy hollows with entrance sizes proportional to their body size to minimise risk of predation, reduce competition at nest sites, and because hollows are of a size that is accessible (e.g. Beyer and Goldingay, 2006; Goldingay and Stevens, 2009)
Tree size	(iii) Nest boxes secured to small (20–50 cm DBH) and medium sized trees (51–80 cm DBH), which support fewer natural hollows, will be occupied more than nest boxes secured to large trees (>80 cm DBH), which support more natural hollows	The number of hollows available at a tree can affect the likelihood of hollow occupancy (e.g. Gibbons et al., 2002; Koch et al., 2008)
Landscape context	(iv) Nest boxes placed in modified landscapes (pasture, urban parklands, urban built-up areas), which support fewer hollow-bearing trees, will be occupied more than nest boxes placed in a semi-natural landscape (reserve), which supports more hollow-bearing trees	The number of hollow-bearing trees available in the landscape can affect the likelihood of hollow occupancy (e.g. Smith and Agnew, 2002; Cockle et al., 2010)
Landscape context	(v) Common adaptable native and exotic species will preferentially occupy nest boxes placed in modified landscapes than nest boxes placed in a semi-natural landscape	Introduced exotic pest and common native species tend to be tolerant of human disturbance and have a high propensity to persist in modified landscapes and exploit limited resources (Lindenmayer et al., 2009; Grarock et al., 2013)

urban development has led to an approximately 95% decline in box-gum grassy woodlands that once dominated this region and is now listed as a critically endangered ecological community (Department of the Environment, 2015). As part of this decline, the loss of large, hollow-bearing trees has been identified as a key threatening process (New South Wales Government, 1995). In southeastern Australia, it is estimated that 17% of bird, 42% of mammal, and 28% of reptile species use natural hollows (Gibbons and Lindenmayer, 1997).

2.2. Experimental design

We stratified our study area into four dominant landscape contexts representing varying degrees of modification and natural hollow availability (Table 2): (1) reserves (semi-natural conservation areas); (2) pasture (grazed agricultural land); and public urban greenspace ($\geqslant$0.2 ha) subdivided into (3) parklands and (4) roadside margins in built-up residential areas. In each landscape context, we randomly selected 12 trees on which to secure nest boxes (nest box trees). Trees were selected from within randomly allocated 20 × 50 m vegetation plots and were located across nine reserves (average (±SE) tree density (per 0.1 ha) = 56.9 ± 9.9; average distance to nearest tree (m) = 6.8 ± 0.9), four rural landholdings (13.3 ± 5.6; 26.5 ± 5.6), 12 urban parklands (16.1 ± 4.4; 12.9 ± 1.6) and 12 urban built-up areas (1.8 ± 0.3; 23.9 ± 4.1), which collectively spanned approximately 50 km^2. All nest box trees were spaced >250 m apart to minimise spatial dependence and were restricted to native *Eucalyptus* species. Tree sizes included: small (20–50 cm diameter at breast height (DBH)); medium (51–80 cm DBH); and large ($\geqslant$80 cm DBH). Therefore, our design constituted four landscape contexts and three tree sizes each with four replicates, resulting in 48 nest box trees. The DBH, height and canopy width of nest box trees in each tree size category did not differ significantly across landscape contexts (p > 0.05; Kruskal–Wallis ANOVAs).

We installed a total of 144 nest boxes. Three nest boxes were secured directly onto each tree (using a wooden panel/backboard and galvanised hardware), which was equivalent to the average number of natural hollows observed at large trees in our study area (Table 2; Fig. S1). Each nest box installed per tree had a different circular entrance size: one small (20 or 35 mm diameter); one intermediate (55 or 75 mm) and one large (95 or 115 mm), which was reflective of the entrance size variations observed for natural hollows at native trees. We established an equal number (n = 24)

Table 2
The abundance (mean ± SE) of natural hollows ($\geqslant$20 mm) with different entrance sizes, at different tree sizes, and in different landscape contexts.

Factor	Natural hollow availability
Entrance size[a]	Hollows/ha
Small (20–50 mm)	15.83 ± 1.91
Medium (51–100 mm)	5.63 ± 0.77
Large (>100 mm)	6.40 ± 0.92
Tree size[b] (Diameter at breast height, DBH)	Hollows/tree
Small (20–50 cm)	0.00 ± 0.00
Medium (51–80 cm)	1.25 ± 0.35
Large (>80 cm)	2.97 ± 0.89
Landscape context[a]	Hollow-bearing trees/ha
Semi-natural reserves	12.1 ± 1.64
Grazed pasture	4.70 ± 0.74
Public urban greenspace ($\geqslant$0.2 ha)	5.70 ± 1.08

[a] Measurements derived using vegetation plots (50 × 20 m; 0.1 ha) conducted at 300 random locations (n = 100 plots/landscape context).
[b] Measurements derived from detailed visual assessments conducted at 120 randomly selected sample trees (n = 30 trees/landscape context; see details described in Le Roux et al., 2014a).

of nest boxes for all six entrance sizes, replicated equally by landscape context and tree size treatments. Each nest box was installed at a different height (3, 4, 5 m) and orientation (north, south, east, west), ensuring that, for each entrance size, an equal number of nest boxes where located at different heights (8 boxes/height) and orientations (6 boxes/orientation), respectively. Nest boxes were of a standard rectangular design made from untreated plywood (mixed hardwood *Eucalyptus* spp.) with equal volumes (0.028 m^3) and dimensions (height 45 cm × width 25 cm × depth 25 cm).

2.3. Data collection

We inspected nest boxes to confirm animal occupancy in 2013 and 2014. We restricted inspections to late winter and early summer (August–December) to maximise detection of animals using nest boxes for breeding over this period. Therefore, we completed ten checks per nest box. Nest boxes were inspected using a wireless camera (Signet, QC8712, Australia) and extension pole (Hastings, E-50, USA), enabling non-invasive observations. 'Occupancy' was defined as an animal being inside a nest box at the time of inspection or conclusive evidence of current occupancy (e.g. nesting material and eggs).

2.4. Data analyses

For all analyses, we pooled data across inspections and survey years. That is, repeated observations of occupancy across inspections were treated as a single occupancy record. We excluded nest boxes (n = 4; 2.7% of nest boxes) where entrance sizes were increased by >10 mm due to gnawing by animals, which resulted in a sample of 140 nest boxes.

2.4.1. Factors affecting overall occupancy
We used a generalised linear mixed model (logit link) to determine whether nest box occupancy was affected by entrance size, tree size and landscape context. We fitted 'entrance size', 'tree size' and 'landscape context' as fixed categorical effects and 'tree identity' as a random effect to account for variation between nest box trees as three nest boxes were installed per tree.

2.4.2. Factors affecting occupancy by common fauna
We used a multinomial logistic regression model to investigate differences in nest box occupancy by common fauna (species that occupied $\geqslant$5% of nest boxes; Table 3). These fauna represented different body size categories and included: the common brushtail possum *Trichosurus vulpecula* (body mass > 2000 g), common exotic birds (common myna *Acridotheres tristis* and common starling *Sturnus vulgaris*; 50–150 g), common native birds (eastern rosella *Platycercus eximius* and crimson rosella *Platycercus elegans*; 50–150 g), and the European honey bee *Apis mellifera* (<2 g). 'No occupancy' was an additional response category. We recorded seven instances where different animal species occupied the same nest box, which we excluded from this analysis resulting in a sample of 133 nest boxes. 'Entrance size', 'tree size' and 'landscape context' were fitted as fixed categorical effects in our starting model and we used an information-theoretic approach to select the model of best fit by ranking models based on Akaike's Information Criterion values (AIC).

3. Results

We found that 69% of nest boxes (n = 99) were occupied by fauna. Twelve species occupied nest boxes, including three mammal species, eight bird species, and one invertebrate species

Table 3
Summary of nest box occupancy by fauna.

Taxonomic group	Common name	Scientific name	Introduced/native	Landscape Context[a]	Tree size (DBH)[b]	Nest box entrance size (mm)	Number of nest boxes occupied
Mammal	Black rat	*Rattus rattus*	Introduced	R, UP, UB	S, M, L	35, 55, 75, 115	5 (3.47%)
Mammal	Common brushtail possum	*Trichosurus vulpecula*	Native	R, P, UP, UB	S, M, L	75, 95, 115	42 (29.16%)
Mammal	Sugar glider	*Petaurus breviceps*	Native	R	S, M	75, 95	2 (1.38%)
Bird	Australian owlet-nightjar	*Aegotheles cristatus*	Native	R	M, L	55, 115	3 (2.08%)
Bird	Australian wood-duck	*Chenonetta jubata*	Native	P, UB	M, L	115	2 (1.38%)
Bird	Common myna	*Acridotheres tristis*	Introduced	R, UP, UB	S, M	55, 75, 95, 115	9 (7.85%)
Bird	Common starling	*Sturnus vulgaris*	Introduced	R, P	S, M, L	55	6 (4.26%)
Bird	Crimson rosella	*Platycercus elegans*	Native	R, P, UP	S, M, L	75, 115	6 (4.26%)
Bird	Eastern rosella	*Platycercus eximius*	Native	R, P, UP	S, M, L	55, 75, 95	7 (4.86%)
Bird	Galah	*Eolophus roseicapilla*	Native	P	M	95	1 (0.69%)
Bird	Sulphur-crested cockatoo	*Cacatua galerita*	Native	P, UP	S, L	75, 115	2 (1.38%)
Invertebrate	European honey bee	*Apis mellifera*	Introduced	R, P, UP, UB	S, M, L	20, 35, 55	18 (12.50%)
Total: occupied							99 (68.75%)
Total: unoccupied							45 (31.25%)
Grand total							144

[a] R = reserve, P = pasture, UP = urban parkland, UB = Urban built-up.
[b] S = small (20–50 cm), M = medium (51–80 cm), L = large (>80 cm).

(Table 3). Six common species accounted for 89% of occupancies (common brushtail possum, common myna, common starling, eastern rosella, crimson rosella, and the European honey bee). The sugar glider *Petaurus breviceps* and Australian owlet-nightjar *Aegotheles cristatus* rarely occupied nest boxes and only in reserves. No species that occupied nest boxes were of conservation concern. Four species were invasive pests (common myna, common starling, the European honey bee and the black rat *Rattus rattus*).

3.1. Factors affecting overall occupancy

Entrance size had a significant effect on nest box occupancy (Wald = 50.13, df = 5, $p < 0.001$; Table S1). More nest boxes with larger entrance sizes (55, 75, 95 and 115 mm) were occupied (an average of 77–96% of nest boxes occupied) than nest boxes with smaller entrance sizes (20 and 35 mm; 25–46%; Fig. 1(i)).

We found no significant effect of tree size (Wald = 0.01, df = 2, $p = 0.99$) or landscape context (Wald = 1.18, df = 3, $p = 0.76$) on nest box occupancy. A near equal number of nest boxes were occupied when secured to small (72%), medium (68%) and large trees (63%; Fig. 1(ii)) and when placed in reserves (64%), pasture (69%), urban parklands (65%) and urban built-up areas (74%; Fig. 1(iii)).

3.2. Factors affecting occupancy by common fauna

Our best supported multinomial model predicting occupancy by common fauna (species that occupied ⩾5% of nest boxes) contained two factors: nest box entrance size and landscape context (Table S2–S4).

Common fauna occupied nest boxes with entrance sizes proportional to their body size. Nest boxes with an entrance of 20 and 35 mm were unoccupied (54% and 82%, respectively; Fig. 2(i)) or occupied by the European honey bee (<2 g; 46%, 18%). Nest boxes with entrances of 55 and 75 mm were unoccupied (30%, 37%) or had limited occupancy by exotic birds (35%, 16%) and common native birds (50–150 g; 20%, 32%). Nest boxes with entrances of 95 and 115 mm were unoccupied (22%, 28%) or predominately occupied by the common brushtail possum (>2000 g; 72%, 61%).

In reserves, nest boxes were unoccupied (45%), or occupied by the common brushtail possum (17%), exotic birds (17%), and the European honey bee (14%; Fig. 2(ii)). In pasture, nest boxes were unoccupied (53%) or occupied by exotic (16%) and common native birds (16%). In urban parklands, nest boxes were unoccupied (45%) or occupied by the common brushtail possum (32%). In urban built-up areas, nest boxes were unoccupied (31%) or occupied by

the common brushtail possum (35%) and the European honey bee (28%).

4. Discussion

The effectiveness of nest boxes as an applied management and biodiversity offset tool remains controversial and in need of empirical research to inform on-the-ground decision-making. We conducted a nest box experiment at multiple scales to test fine, local and landscape-level effects on nest box occupancy. Entrance size had a significant effect on overall occupancy. Therefore, we advocate that practitioners should not overlook fine-scale nest box design attributes such as entrance size at the construction phase of nest box programs (see also other recent studies by Lambrechts et al., 2012; Rueegger et al., 2013; Goldingay et al., 2015; Lindenmayer et al., 2015). However, tree size and landscape context did not affect overall occupancy, suggesting that nest boxes can offer nesting opportunities to species, even when secured to smaller sized trees or when placed in disturbed environments. Common fauna occupied nest boxes in non-random ways, preferentially occupying nest boxes: (1) with entrance sizes proportional to their body size; and, for some species, (2) when located in specific landscapes contexts (urban environments). Overall, nest boxes were occupied only by a few common native and exotic species. Our findings suggests that nest boxes are unlikely to be a highly effective management and biodiversity offset tool for a multitude of hollow-dependent species, including rare and threatened taxa of highest conservation concern, particularly in landscapes characterised by increased modification. However, several case studies have highlighted the relative success of nest box programs for some threatened species in different landscape contexts (e.g. Libois et al., 2012; Olah et al., 2014; Goldingay et al., 2015).

4.1. Spatial factors affecting occupancy

As expected, nest boxes with larger entrance sizes were occupied more than nest boxes with smaller entrance sizes. Small natural hollows (20–50 mm) can form even in relatively young trees (small and medium trees) and thus tend to be more abundant compared to large natural hollows (>50 mm), which can take much longer to form, typically only in large old trees (Lindenmayer et al., 1993; Blakely et al., 2008). Therefore, small hollows may be in less demand compared to large hollows which are often a limiting resource for many hollow-using species (e.g. Newton,
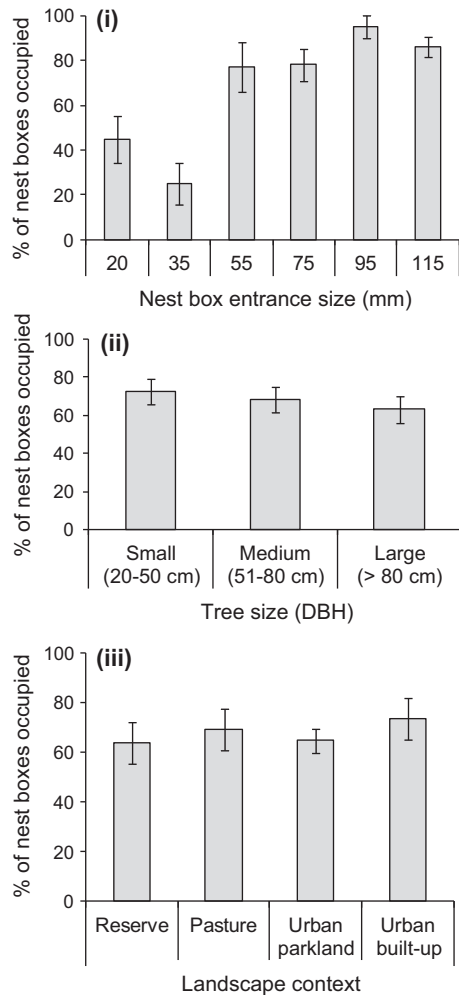
Fig. 1. Percentage (mean ± SE) of nest boxes (*n* = 140) occupied: (i) with different entrance sizes (20, 35, 55, 75, 95, 115 mm); (ii) when secured to trees of different sizes (small, 20–50 cm DBH; medium, 51–80 cm; large, >80 cm); and (iii) when placed in landscape contexts with varying degrees of modification (reserves, pasture, urban parklands, urban built-up areas).

Fig. 2. Percentage of nest boxes (*n* = 133) occupied by common fauna (species that occupied ⩾5% of nest boxes) that: (i) had different entrance sizes (20, 35, 55, 75, 95, 115 mm) and (ii) were placed in different landscape contexts (reserves, pasture, urban parklands, urban built-up areas). Response categories included occupancy by: the common brushtail possum (>2000 g), exotic birds (50–150 g), common native birds (50–150 g), and the European honey bee (<2 g). 'No occupancy' was an additional response category.

1994; Manning et al., 2004; Durant et al., 2009; Goldingay et al., 2015). Furthermore, a wide range of hollow-nesting animals (e.g. most hollow-nesting birds and arboreal mammals) may simply not be able to access nest boxes with very small entrances (Gibbons and Lindenmayer, 2002).

Although not tested in our study, other nest box design attributes can also affect occupancy, including nest box volume, placement height, orientation and the types of construction materials used (Harper et al., 2005; Ardia et al., 2006). For example, insectivorous bats (Microchiroptera) tend to occupy nest boxes with narrow internal dimensions and slit entrances located at the base of nest boxes (Smith and Agnew, 2002; Flaquer et al., 2006). This may explain why bats were not observed using nest boxes in our study. Similarly, some threatened hollow-nesting species may require custom-designed nest boxes with specific attributes that more closely mimic natural hollows selected by individuals (Bolton et al., 2004; Brazill-Boast et al., 2013; Goldingay et al., 2015).

Common species preferentially occupied nest boxes with entrance sizes proportional to their body size. Preference for hollows with entrance sizes just large enough for an animal to access may be driven by selection pressures like predation and competition over limited nest sites. For example, Hakkarainen and Korpimäki (1996) suggested that small bodied Tengmalm's owls
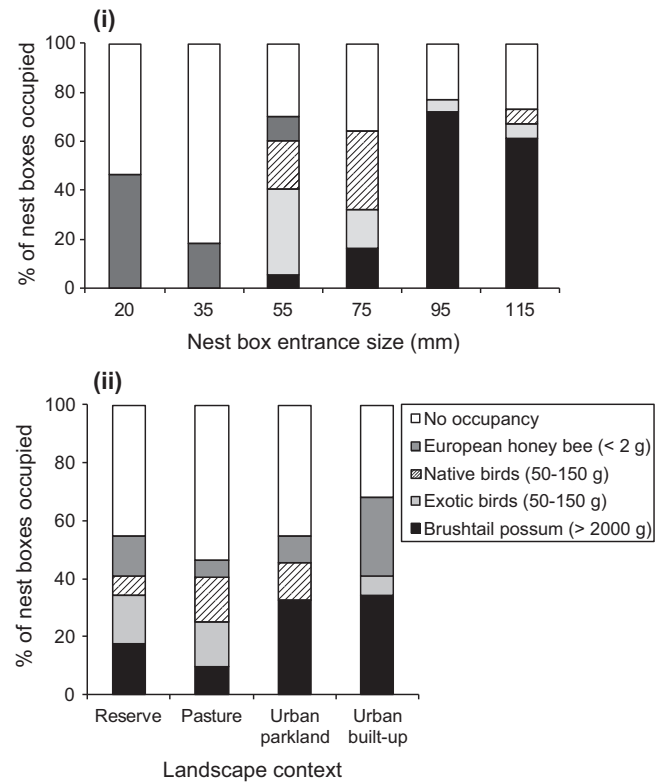
Aegolius funereus in Finland avoided using nest boxes with entrances >115 mm due to risk of predation and competition by larger Eagle owls *Bubo bubo* and Ural owls *Strix uralensis*. In our study, it is possible that the common brushtail possum, which occupied 65% of nest boxes with large entrances (>95 mm), precluded other species from using nest boxes with large entrance sizes (Harper et al., 2005). This, in turn, may have facilitated increased conspecific competition between native and exotic birds at nest boxes with intermediate entrance sizes (Davis et al., 2013).

Although we did not measure occupancy at natural hollows, we hypothesised that animals would preferentially occupy natural hollows over nest boxes where hollows were locally abundant at large trees (c.f. small and medium trees). Natural hollows tend to have a wider range of characteristics and potentially offer greater thermoregulatory benefits to species than nest boxes (McComb and Noble, 1981). However, we found that tree size had no significant effect on overall nest box occupancy. This is counter to other studies that have found that nest boxes secured to smaller sized trees were more likely to be occupied than when secured to larger trees, possibly owing to a lack of natural hollows at smaller trees (Durant et al., 2009). One explanation for our result may be that not all large trees supported a large number of natural hollows or hollows that were suitable for occupancy (Gibbons et al., 2002). For example, in urban environments, large trees may support few hollows due to tree management practices that remove dead and hollow-bearing branches for public safety (Carpaneto et al., 2010; Le Roux et al., 2014b). Studies on natural hollows have found that animal occupancy was more likely at trees that supported many visible hollows (Webb and Shine, 1997; Gibbons et al., 2002; Koch et al., 2008). We found no evidence of a similar

trend occurring for nest boxes. Future studies could more closely investigate the relationship between structural tree attributes and nest box occupancy as recent research suggests that certain animal groups (e.g. hollow-nesting birds) may be particularly attracted to larger trees that have been enriched with nest boxes (Le Roux et al., 2015a).

Landscape context had no significant effect on overall nest box occupancy, which is counter to others studies that have reported only limited occupancy of nest boxes in environments with an abundance of hollow-bearing trees (Smith and Agnew, 2002; Lindenmayer et al., 2009). One explanation for our result is that temperate woodland habitats, like those in our study area, tend to support lower overall densities of hollow-bearing trees (7–17 hollow-bearing trees/ha) compared with habitats like temperate rainforests (13–27 hollow-bearing trees/ha; Gibbons and Lindenmayer, 2002). This may have resulted in more extreme differences in hollow availability and a greater discrepancy in nest box occupancy between unmodified and modified locations in other study environments compared to our own study location where hollow-bearing tree availability was more graded across landscape contexts (Table 2). Some animal species are known to occupy nest boxes only in areas where natural hollows are abundant or where habitat connectivity is increased, which may facilitate colonisation of nest boxes by some species (Menkhorst, 1984; Lindenmayer et al., 2015). In our study, the sugar glider and the Australian owlet nightjar occupied nest boxes only in semi-natural reserves where the highest densities of hollow-bearing trees were recorded. Therefore, the probability of nest boxes being occupied may simply be due to the likelihood of a species being present and encountering nest boxes in a given environment. Similar rates of nest box occupancy across landscape types in our study are also likely due to the ubiquitous nature of common native and exotic species that predominately occupied nest boxes.

We found strong evidence that common adaptable native and exotic species exploit nest boxes in all landscape contexts investigated in our study. The European honey bee showed a preference for occupying nest boxes in urban built-up areas, which is somewhat unsurprising given that this generalist pollinator is known to exploit resources (e.g. flowering garden plants) in residential areas (e.g. Threlfall et al., 2015). Interestingly, few nest boxes were occupied by exotic birds and rarely so in urban environments, which is a result counter to findings from other studies conducted in the same study area (Pell and Tidemann, 1997; Grarock et al., 2013). Recent eradication programs targeting exotic birds in suburban areas of Canberra (particularly the common myna) may explain lower than expected occupancy of nest boxes by exotic birds (Grarock et al., 2014). The common brushtail possum (often regarded as a native 'pest' in urban areas) showed a strong preference for occupying nest boxes in urban environments, a result congruent with other studies (e.g. Harper et al., 2005).

4.2. Considerations for management and biodiversity offsets

Where nest boxes are used to achieve no-net-loss of habitat as part of a biodiversity offset requirement (Lindenmayer et al., 2009; Peste et al., 2015), we suggest that the minimum compensation required for the unavoidable loss of each hollow-bearing tree should be multiple nest boxes with different entrance sizes (Lambrechts et al., 2012; Rueegger et al., 2013; Goldingay et al., 2015; Lindenmayer et al., 2015). A single large, hollow-bearing tree typically supports many hollows with a range of entrance sizes that provide a diversity of nesting opportunities for numerous species (Gibbons et al., 2002; Koch et al., 2008; Cockle et al., 2011; Le Roux et al., 2014b). Multiple nest boxes with different entrance sizes more accurately reflects the availability of natural hollows as they occur naturally at hollow-bearing trees (Lindenmayer

et al., 1991). We caution against a 'one-size-fits-all' approach because this has the potential to exclude certain species from occupying nest boxes and enable others to potentially exploit nest boxes. This could result in an increase in the population size or range expansion of dominant or problematic species and further exacerbate shortages in natural hollows by increasing competition at limited nest sites (Pell and Tidemann, 1997; Lindenmayer et al., 2009; von Post and Smith, 2015).

Some characteristics of hollows are difficult to replicate artificially, especially on a large scale (e.g. hollows that are very deep, shallow, wide, narrow or located very high). Hollow-bearing trees also provide other critical habitat structures (e.g. fallen logs, dead branches, large living lateral branches, and peeling bark microhabitat) that many species depend on for survival and can take as long to form as natural hollows (Manning et al., 2006; Lindenmayer et al., 2013). Therefore, management and offset programs that only use nest boxes as replacement habitat for the loss of large trees are unlikely to benefit many species, including species with specialist hollow requirements or species that depend on other habitat structures provided by large trees.

We found that six common native and exotic species accounted for 89% of nest box occupancies and no species of conservation concern occupied nest boxes despite threatened hollow-nesting species occurring in our study area, including in modified landscapes (e.g. superb parrot *Polytelis swainsonii*). Paradoxically, nest boxes are often employed to compensate threatened hollow-nesting species most at risk of being impacted by human activities (Goldingay and Stevens, 2009; Lindenmayer et al., 2009). This is despite only limited empirical evidence demonstrating that targeted threatened species will occupy nest boxes in a capacity that can benefit local populations over the long-term (see Goldingay et al., 2015). These efforts typically require nest box locations and designs to be highly targeted, which often only focus on a single threatened species or species group (e.g. Libois et al., 2012; Rueegger et al., 2013; Olah et al., 2014).

A further consideration is the rapid rate of nest box attrition. Even within two years, we recorded the loss of five nest boxes (3.5%). Nest box attrition (with a conservative estimated 'lifespan' of 10 years per nest box) may exceed the time it takes for some animal species to locate and occupy nest boxes (Lindenmayer et al., 2009; but see Goldingay et al., 2015). In contrast, natural hollows likely persist over much longer time periods (Gibbons et al., 2000; Ranius et al., 2009). Efforts to maximise the durability of nest boxes over longer time periods could involve improvements to construction materials, attachment methods, and removing certain species (e.g. European honey bee hives) from nest boxes (Beyer and Goldingay, 2006; Goldingay et al., 2015). The efficacy of nest box programs also needs to be balanced against the financial costs associated with materials, monitoring, maintaining and replacing nest boxes over the long-term (McKenney and Lindenmayer, 1994; Harper et al., 2005). In our study, the expense of construction materials, labour, travel and monitoring 144 nest boxes over two years was approximately AUD$ 13,608 ($94 per nest box ($40 for materials and $27 per year for monitoring)).

We recommend that, when used in isolation, nest boxes are unlikely to be highly effective management and biodiversity offset tools. This is because: (1) the attributes of natural hollows and other habitat structures provided by large, hollow-bearing trees (e.g. fallen logs) cannot be easily replicated; (2) there is a high probability that there will be a lack of equivalence between trees removed (losses) and nest boxes added (gains), both in availability (number of nest boxes added as compensation) and functionality (number of nest boxes occupied by targeted species); and (3) there is little confidence that nest boxes can effectively ameliorate the loss of natural hollows by providing long-term benefits for many hollow-dependent species, especially rare and threatened taxa that

face the highest risk of population decline and extinction in the interim.

We encourage policymakers and managers to place a greater emphasis on mitigating and avoiding the loss of large, hollow-bearing trees. Priority should be given to retaining trees that support multiple hollows with a variety of entrance sizes and characteristics that likely benefit many species (Gibbons and Lindenmayer, 2002). As an example, new urban developments could be planned so that a greater proportion of existing trees are safely retained and managed in urban greenspace rather than simply being removed (Stagoll et al., 2012; Barth et al., 2015; Ikin et al., 2015; Le Roux et al., 2015b). Accelerating the formation of hollows by other means (e.g. carving out hollows with chain-saws), or creating nest boxes that more closely mimic the characteristics of natural hollows also still warrants further experimentation (Bull and Partridge, 1986; Lewis, 1998; Jansson et al., 2009).

Based on our findings, we caution against the wide-scale implementation of nest box programs, which still require further research aimed at increasing their effectiveness. Nest box supplementation should be considered only as an interim management strategy undertaken in conjunction with other mitigation and avoidance tactics, such as limiting the removal of established hollow-bearing trees in modified environments. Manipulating nest box entrance size and placement in the landscape can effectively exclude or encourage occupancy by common hollow-nesting species, which could have other important implications for wildlife management (e.g. studying the breeding ecology of hollow-using species; Mainwaring, 2011; Wiebe, 2011; Björklund et al., 2013). Nest boxes may also play a vital role in education and in improving ecosystem functioning even when occupied by common native and exotic species (e.g. crop pollination by European honey bees).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.02.017.

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