

# Modelling Tree Hollow Availability Over Time in the Barmah Landscape Zone

## A Report to the Goulburn-Broken CMA

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## **Executive Summary**

Existing data sets and some limited on-the-ground surveys of hollows in river red gums at a variety of sites in Barmah Forest were used to evaluate availabilities of tree-hollows of three sizes. Extensive consultations were made to track down pertinent data sources.

We used hierarchical Bayesian models to link probabilities of trees bearing any hollows and hollow numbers to tree diameter and growth rates.

Future projections of hollow availabilities were made using the growth-rate mediated models.

Experienced faunal ecologists in river red gum forests made assessments of the species of vertebrates likely to be affected by changes in hollow availability.

Given documented declines in growth rates of river red gums in face of prolonged water deprivation, it seems that there needs to be a thorough re-evaluation of what constitutes potentially “sustainable” harvesting amounts in the Barmah Forest. The strong dependence of hollow availability and tree diameter, and the sharp decrease in growth rates since the mid-1990s, suggest that active management is necessary to ensure that sufficient numbers of existing large trees and trees recruiting into mid-size and large size classes in the future are available.

Growth rates may need to be actively “encouraged” by enforcing appropriate floodplain inundation and perhaps by ecologically thinning areas to reduce water and resource competition.

There are insufficient data to evaluate factors affecting population viability of hollow-dependent fauna. Some of the most threatened fauna may be suffering from whole-landscape collapse in availability of resources upon which they depend.

## Introduction

Two of the primary biodiversity goals of the Goulburn-Broken Regional Catchment Strategy are to improve the quality of existing native vegetation by 10% and to enhance the conservation status of the majority of threatened fauna by 2030.

The extensive area of Barmah forest has the potential to support a large number of hollow-dependent fauna (Chesterfield et al. 1984, Loyn et al. 2002). Despite information suggesting that there are about a hundred useable habitat hollows per hectare in these large tracts of forest (Newton-John 1992) evidence suggests that densities of hollow-dependent fauna are low (Mac Nally et al. 2001). Densities of fauna species dependent on large volumes of fallen timber are also low compared with similar habitats elsewhere (Mac Nally et al. 2001).

It is possible that larger populations of hollow-dwelling animals may be able to establish within this region if the habitat improves. For example, Mac Nally and Horrocks (2002) increased local densities of Yellow-footed Antechinus (*Antechinus flavipes*) and Brown Treecreeper (*Climacteris picumnus*) in forest similar to Barmah at Gunbower Island by providing more fallen timber. Lada et al. (2007) showed that trapping rates (a measure of local abundance) of *A. flavipes* was jointly influenced by proximity to floods, fallen timber loads and numbers of large trees. The latter presumably reflects presence of hollows. A critical question is whether populations of hollow-dependent fauna presently are limited by the availability of hollows, or by other limiting resources or processes.

The region is characterized by a number of hollow-dependent nationally threatened species including Superb Parrot (*Polytelis swainsonii*), and several species listed as threatened in Victoria [e.g. Barking Owl (*Ninox connivens*), Squirrel Glider (*Petaurus norfolcensis*), Brush-tailed Phascogale (*Phascogale tapoatafa*), Southern Myotis (*Myotis macropus*), Tree Goanna (*Varanus varius*) and Carpet Python (*Morelia spilota*)] (Emison et al. 1987, Menkhorst 1995, DSE 2003). Fallen timber generated from large, hollow-bearing trees also provides important habitat for other threatened species including Grey-crowned Babbler (*Pomatostomus temporalis*) and Bush Stone-curlew (*Burhinus grallarius*).

The provision of hollow-bearing trees in this region therefore is critical to maintaining viable populations of species and achieving conservation goals for the Goulburn-Broken catchment.

## Background

Native Australian trees do not usually develop hollows until they are very old at which time they may be selectively used by vertebrate species for nest and roost sites (Gibbons and Lindenmayer 2002, Cameron 2006, Kalcounis-Ruppell *et al.* 2006). In particular larger hollows, critical to owls and cockatoos, generally do not develop until trees are > 100 years old (Vesk *et al.* 2008). Development of suitable large hollows is regarded as being a characteristic feature of tree senescence (Jacobs 1955; Ambrose 1979; Mackowski 1984; Perry *et al.* 1985; Inions *et al.* 1989) but the process can be accelerated through disease and or damage to the tree (Gibbons and Lindenmayer 2002).

In many eucalypt species the presence, abundance and size of hollows have been correlated with tree basal diameter (Lindenmayer *et al.* 1991, Bennett *et al.* 1994, Vesk *et al.*, 2008) but this relationship has not been well established for the river red gum (*Eucalyptus camaldulensis*). While it is reasonable to assume that large old river red gums are more likely to contain an increased number of different sized hollows, variable growth rates and propensity to drop limbs makes it difficult to define a clear relationship between basal diameter and number of hollows present.

We expect that, as with other eucalypt species (Soderquist 1999, Gibbons and Lindenmayer 2002), large old river red gums are more likely to contain increased numbers of hollows of various size classes. Although rare, these large hollow-bearing trees would be selectively used by vertebrate species for nest and roost sites similar to other eucalypts (Gibbons *et al.* 2002, Cameron 2006 Kalcounis-Ruppell *et al.* 2006)

The locations and spatial configuration of hollow-bearing trees within the landscape can also be an important consideration. Certain vertebrate species prefer locations close to riparian habitat (Law and Anderson 2000) or suitable foraging areas (Kavanagh and Wheeler 2004), while others, particularly colonial nesters, prefer clustered sites for breeding (Gibbons and Lindenmayer 2002, Cameron 2006). A more even spread of hollow-bearing trees is required for strongly territorial species, such as cockatoos, which prevent other breeding pairs from nesting nearby (Rowley and Chapman 1991)

For a number of reasons that may include lowering the risk of predation, nest hygiene or temporal proximity to resources, many species use more than a single hollow over time (Nilsson 1984, Lewis 1995). While most birds will use a single hollow during the nesting season (Newton 1994) several mammal species, particularly bats, require multiple hollows of suitable size and shape (Cockburn and Lazenby-Cohen 1992, Lumsden *et al.* 2002, Rhodes *et al.* 2006).

Given that many vertebrates are known to select hollows according to specific characteristics, mere number of hollows may not be a good indication of available resources (Newton 1994). A major consideration is how entrance dimensions relate to body size for both access and exclusion of larger competitors/predators (Tiedemann and Lavel 1987, Dickman 1991 and Harley 2004). Several factors may be of importance in hollow selection, depending on the animal species involved, including orientation, height, depth, exposure, thermal insulation and surrounding cover (Menkhorst 1984).

Several studies have reported correlations between abundance and diversity of hollow-using species and the density of hollow-bearing trees (Meredith 1984, Smith and Lindenmayer 1988, Traill 1991, Newton 1994, Kavanagh and Stanton 1998, Alexander *et al.* 2002, Kavanagh and Wheeler 2004). The density of hollow-bearing trees required to maintain species diversity is a function of the range of hollow-using species at a site, their densities, number of hollows required by individuals and the number and configuration of suitable hollows within individual trees. Few studies have quantified the actual densities of hollow-bearing trees required to sustain viable populations even of single species, let alone of entire assemblages. The data requirements for such analyses are extensive.

Experimental manipulation of hollow availability has demonstrated that availability of hollows can alter the densities of mammals, birds and bats (Gibbons and Lindenmayer 2002, Beyer and Goldingay 2006), but no such studies have been conducted in river red gum forests.

Large old hollow-bearing river red gums can provide additional resources for resident fauna by exhibiting a greater propensity to provide food resources including flowers, nectar, fruit, seeds, leaves and insects (Recher 1996). They can also provide valuable foraging substrates and shelter sites in the event of collapse or limb drop (Scotts 1991, Mac Nally *et al.* 2001). Several threatened predatory species are reliant on hollow-dwelling prey and the loss of suitable hollows is likely to result in a decline in this food resource (Robinson 1989, Milledge & Palmer 1990).

Similar to other Victorian hardwood forests used for timber and firewood production, both historical and contemporary silvicultural practices have greatly reduced the number of hollow-bearing trees (Ross 1991, Lindenmayer *et al.* 1991 and Smith *et al.* 1994). Predictive modelling of hollow-bearing trees retained after harvesting in other production forest suggests a long-term reduction in densities of mature trees due in part to post-harvest mortality (Gibbons 1999).

Loss of hollow-bearing trees has been listed as a threatening process under both the Flora and Fauna Guarantee Act in Victoria and the Threatened Species Conservation Act in New South Wales. The continuing net loss of hollow-bearing trees in native forests and woodlands due to firewood harvesting practices has been nominated and recommended for listing as a Key Threatening Process under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999.

Emison *et al.* (1987) consider 16 species of mammal and 44 species of bird including 14 mammals and birds considered threatened in Victoria (DSE 2003) as being dependent on hollows. The Tree Goanna (*Varanus varius*) also is dependent upon hollows for shelter (Scotts 1991). Gibbons and Lindenmayer (2002) suggested that in NSW at least 46 mammals, 85 birds, 32 reptiles and 16 frogs are reliant on tree hollows for shelter and nests. Of the 45 hollow-dependent species listed as threatened on Schedule 1 and Schedule 2 of the Threatened Species Conservation Act fifteen are known to occur in or around the Barmah area (Appendix).

Here, we use a range of existing data on tree growth and hollow availability to make assessments of the current availability and future prospects for hollow availability for dependent (vertebrate) species in river red gum forests at Barmah. We address the following questions:

- Which hollow-dependent fauna species are using the remnant habitat?
- Is the abundance of hollows for hollow-dependent fauna likely to be maintained in the future?
- What is the contribution of human-induced habitat loss to the loss of hollow-bearing trees in this ecosystem?
- What actions are required to maintain or increase the availability of hollow-bearing trees in this ecosystem?

## Methods

### Data sources

Three days were spent collecting data for diameter at breast height (DBH) and number of hollows in river red gum stand at Barmah Forest. These included nine Biological Intact Sites Supporting Clusters of Large Old Trees (BISSCLOT) / Continuous Forest Inventory (CFI) locations in Barmah State Forest and four other sites in Barmah State Park (Figs 1, 2). CFI plots are evenly spaced across Barmah and sample stand attributes (relative stand age and predominant crown size) in approximate proportion to their mapped extents for the Statewide Forest Resource Inventory (SFRI). Harper *et al.* (2005) found that ground surveys were a reliable, if conservative method of identifying hollow-bearing trees.



Additional data were collated from

- structural measurements, including number of hollows present, from seven 2 ha sites in the original pilot course woody debris study (Mac Nally et al. 2001)
- the Continuous Forest Inventory project as part of the SFRI (Fiona Hamilton)
- information supplied by Peter Black from the BISSC Large Old Tree project as part of SFRI.
- unpublished records from Dr Rodney van der Ree, ecologist with the Australian Research Centre for Urban Ecology
- vegetation survey including DBH and presence of hollows in eucalypts at thirty-six 2 ha sites from Gunbower State Forest (Mac Nally and Horrocks 2002)
- unpublished eucalypt measurements Mr M. Looby, PhD University of Melbourne
- data on hollow-bearing tree (HBT) density obtained from Bennett et al. (1994) and Lumsden et al. (2002).

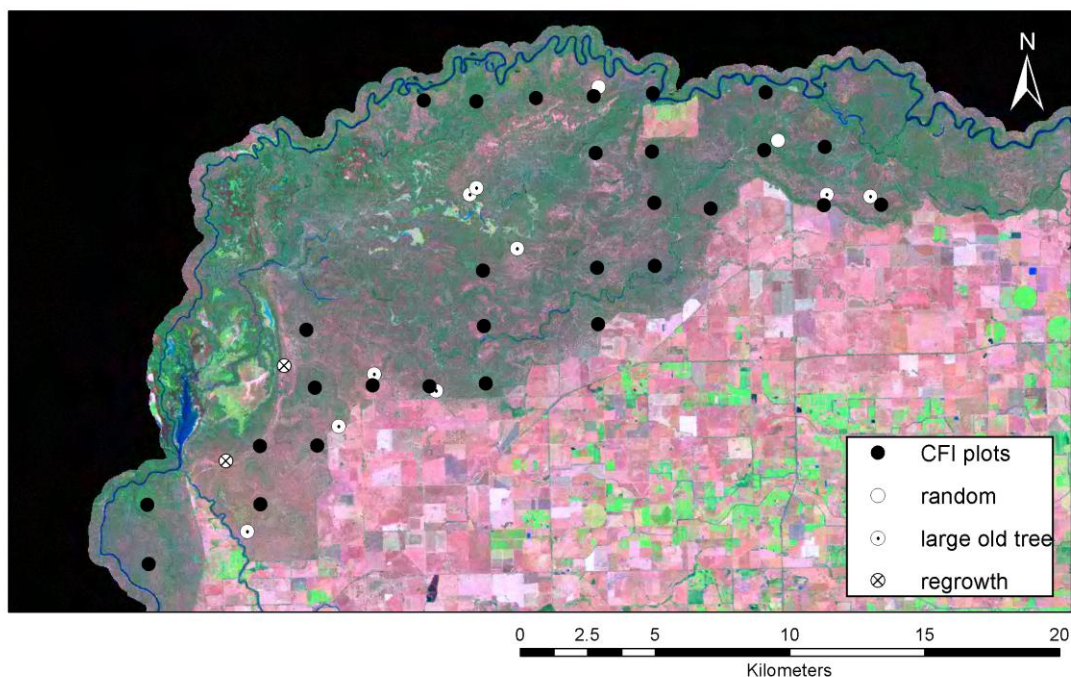


Figure 1. Satellite TM image of Barmah forest with location of continuous forest inventory (CFI) plots and sites surveyed for hollow-DBH data by the authors in 2007. Only CFI plots located and surveyed by D.S.E. staff in 2007 are shown (updated locations of remaining CFI plots were unavailable).

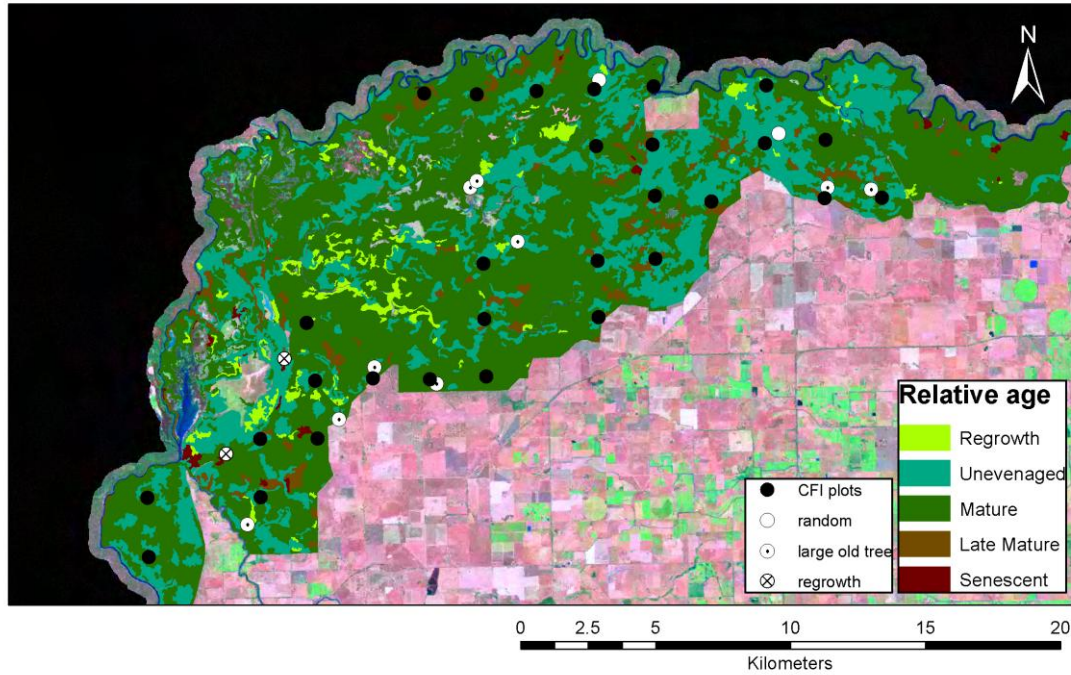


Figure 2. Statewide Forest Resource Inventory (SFRI) forest stand classifications for Barmah. Courtesy D.S.E.

## Analysis

Hollow development in river red gums is a complex and stochastic process. Modelling hollow availability as a function of tree age and environmental factors is complicated by the lack of longitudinal studies of hollow development, and the difficulty of ageing river red gums. Here we develop probabilistic models based on empirical relationships between hollows and tree size (diameter-at-breast-height, DBH) and between tree growth and key environmental factors. Numerous studies have found strong relationships between diameters and the number and size of hollows present in eucalypt species (e.g. Gibbons and Lindenmayer 2002).

We modelled three hollow size-classes separately, using identical model structures: small hollows (<5 cm diameter), medium hollows (5–15 cm diameter) and large hollows (>15 cm diameter).

### **Model 1: Probability of hollows**

We used a binomial model with logit link (i.e. logistic regression model) to model the probability that a tree of a given DBH would bear any hollows of size class  $s$ . The model for the presence (1) or absence (0) of hollows of size class  $s$  in tree  $i$  in plot  $j$ ,  $H_{sij}$ , was:

$$H_{sij} \sim \text{Bernoulli}(p_{sij})$$

$$\text{logit}(p_{sij}) = \alpha_s + \beta_s \times \text{DBH}_i + \varepsilon_j$$

Here  $\alpha_s$  is the intercept,  $\beta_s$  is the slope (change in log odds associated with 1 cm increase in DBH),  $\text{DBH}_i$  is the DBH of tree  $i$ ,  $\varepsilon_j$  is a plot level random term. We assigned uninformative, hierarchical prior distributions to all parameters, as follows:

$$\alpha_s \sim N(0, \sigma_0^2)$$

$$\sigma_1^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

$$\beta_s \sim N(0, \sigma_1^2)$$

$$\sigma_2^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

$$\varepsilon_i \sim N(0, \sigma_3^2)$$

$$\sigma_3^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

Note that the parameters for each size class ( $\alpha_s, \beta_s$ ) shared common variance parameters. This specification was used to shrink parameters to prevent separation (infinite likelihoods), which occurs when the predictor variable(s) discriminate the response very well (Heinze & Schemper 2002). Without such shrinkage the parameters could not be estimated.

### **Model 2: Number of hollows per tree**

We assumed a Poisson distribution for the number of hollows per tree, and modelled the mean (expected) number of hollows as a non-linear function of DBH using a log link and a Bayesian spline model. We included “plot” (stand) level random errors to account for spatial autocorrelation (i.e. within-plot similarities among trees) and “tree” level random errors to account for possible “over-dispersion” in the Poisson model. The model for the number of hollows in size class  $s$  observed in tree  $i$  in plot  $j$   $Y_{sij}$ , was:

$$Y_{sij} \sim \text{Poisson}(\lambda_{sij})$$

$$\log(\lambda_{sij}) = \beta_s + f_s(\text{DBH}_i) + \rho_j + \varepsilon_i$$

where  $\beta_s$  is the intercept for size class  $s$ ,  $f_s()$  denotes a non-linear (spline) function,  $\rho_j$  is the mean error for plot  $j$ , and  $\varepsilon_i$  is the “extra-Poisson” error associated with tree  $i$ . Random error terms  $\rho_j$  and  $\varepsilon_i$  were drawn from normal distributions with zero mean and variances  $\sigma_{plot}^2$  and  $\sigma_{tree}^2$ , respectively. All parameters were given uninformative prior distributions as follows:

$$\beta_s \sim N(0, 1000)$$

$$\rho_j \sim N(0, \sigma_2^2)$$

$$\sigma_2^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

$$\varepsilon_i \sim N(0, \sigma_3^2)$$

$$\sigma_3^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

$$\gamma_n \sim N(0, \sigma_1^2)$$

$$\sigma_1^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

$\gamma_n$  is the  $n^{\text{th}}$  of  $k$  spline parameters (corresponding to  $k$  knots)

$k \sim \text{dpois}(5) | 20$  (a truncated Poisson distribution with mean 5 and maximum 20)

Details of Bayesian spline models can be found in Lunn et al. (2005).

### **Model 3: Tree growth**

We used a two-parameter exponential growth model to relate the increment in DBH of individual trees over sampling intervals (5 to 11 year intervals from 1961 to 2006) to average stem density



and average water depth. The model for the increment in DBH for tree  $i$  in plot  $j$  between dates  $t-1$  and  $t$  was:

$$\Delta_{tij} = (DBH_{\max} - DBH_{i(t-1)})(1 - e^{(-R_{tij}T_t)})$$

$$\log(R_{tij}) = \beta_0 + \beta_1 \times \text{density}_{tij} + \beta_2 \times \text{water}_{tij} + \beta_3 \times \text{density}_{tij} \times \text{water}_{tij} + \nu_j + \omega_i$$

Here  $DBH_{\max}$  is the (estimated) maximum DBH,  $DBH_{i(t-1)}$  is the DBH of tree  $i$  at the previous measurement date,  $T_t$  is the growth interval (time in years between dates  $t-1$  and  $t$ ), and  $R_{tij}$  is the modelled growth parameter for tree  $i$  in plot  $j$  over that period. In the log-linear model for  $R_{tij}$ ,  $\beta_0$  is the overall mean,  $\beta_1$  is the average effect of stem density (sum basal area at date  $j$ ),  $\beta_2$  is the average effect of groundwater depth (estimated average groundwater depth over the interval  $j-1$  to  $j$ ),  $\beta_3$  is an interaction effect, and  $\nu_j$  and  $\omega_i$  are plot and tree level random effects, respectively. The log link function ensures  $R$  (growth rate) is always positive. We specified uninformative prior distributions for all parameters as follows:

$$DBH_{\max} \sim N(0, 1000)$$

$$\beta_0 \sim N(0, 1000)$$

$$\beta_1 \sim N(0, 1000)$$

$$\beta_2 \sim N(0, 1000)$$

$$\beta_3 \sim N(0, 1000)$$

$$\nu_j \sim N(0, \sigma_1^2)$$

$$\sigma_1^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

$$\omega_i \sim N(0, \sigma_2^2)$$

$$\sigma_2^2 \sim \text{inverse-gamma}(0.001, 0.001)$$

Models 1 and 2 were parameterized with data from 323 trees across 13 plots collected by the authors in 2007. Model 3 was parameterized using CFI data (n trees over 29 plots measured in 1961, 1965, 1978, 1987, 1995, and 2006) and water table data derived from groundwater bores in Barmah. We estimated mean groundwater depths by first averaging values for each bore for each time period and then kriging (a geostatistical spatial estimation process, Cressie 1993) those values to create a mean groundwater depth surface (i.e. GIS raster) for each time period.

Models 1 and 2 were combined with model 3 to form hierarchical predictive models for the number of hollows per tree (Model 1 + 3), or proportion of hollow-bearing trees (Model 2 + 3), as a function of tree age, stand density (sum basal area) and average water table depth. Combined models were used to make predictions about hollow provisions through time under different growth conditions (density and water table depth).

## Results

### *Relationship between tree size (DBH) and hollows*

There is a strong relationship between tree DBH and the presence (Figure 3) and number (Figure 4) of hollows in each size class. While the size and number of hollows may vary considerably among trees of similar size (Table 4, Figures 3 & 4) the mean (expected) number of hollows clearly increases with DBH (Figure 4). Across 13 plots throughout Barmah, we found no trees with DBH < 50 cm that contained a habitat hollow, while all but one tree > 100 cm DBH contained at least one habitat hollow. Large hollows were not observed in trees < 73 cm DBH and were generally less likely to be present, and numerically less than smaller hollows when present. Newton-John (1992) found similar relationships between DBH and number of hollows for river red gum in Barmah. The relationship between DBH and probability of hollows in river red gum is similar to that found for other eucalypts (e.g. Bennett et al. 1994, Gibbons and Lindenmayer

2002), but river red gums tend to attain larger diameters and have greater propensity to drop limbs, so mature trees are more likely to have hollows.

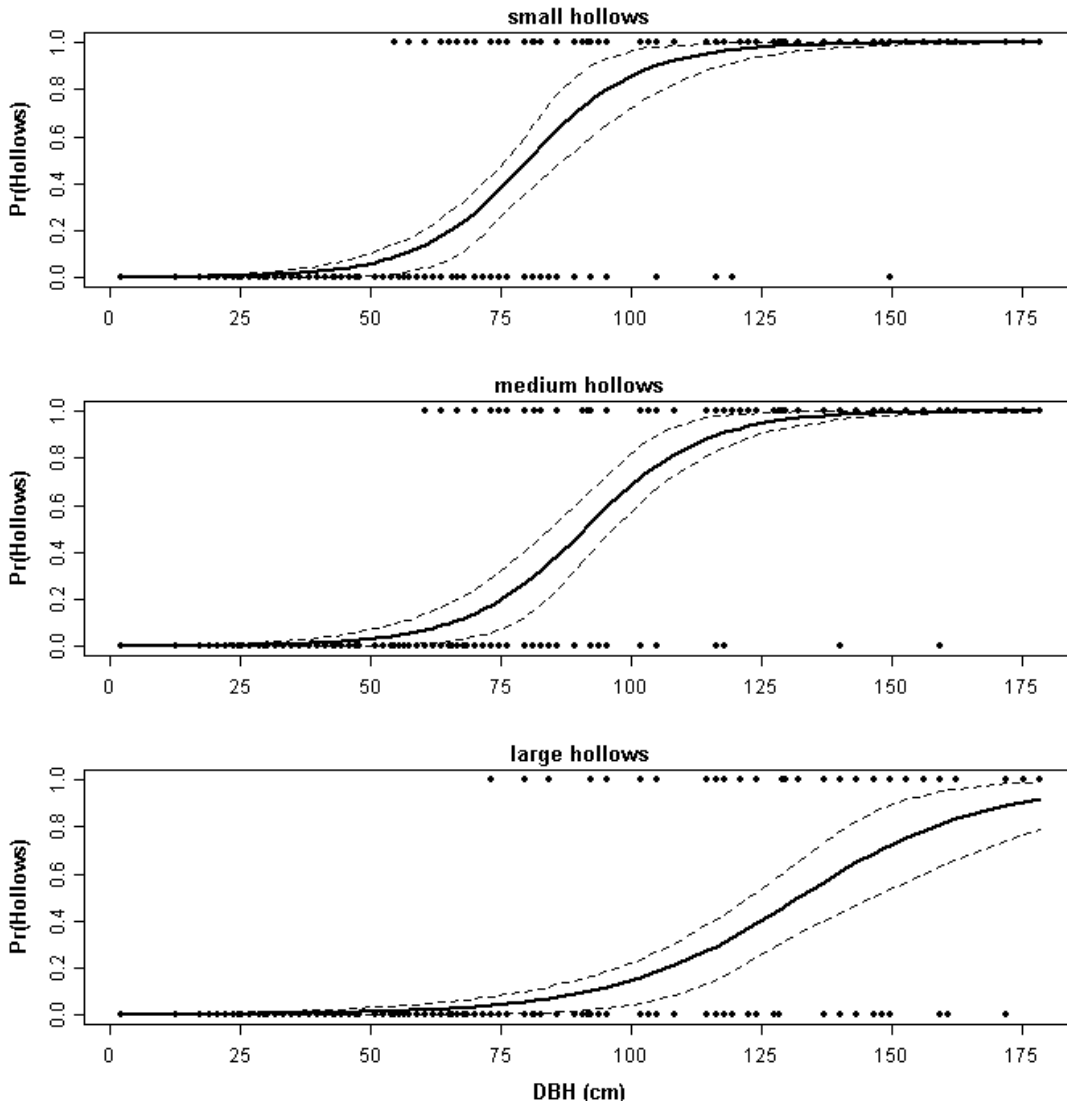


Figure 3. Relationship between tree size (over-bark diameter at breast height, DBH) and the presence of hollows in each of three size classes (small = < 5 cm diameter hole, medium = 5 < diameter < 15, large = diameter > 15 cm). Solid lines are posterior mean probability of hollows being present derived from Bayesian logistic regression model. Dashed lines 95% credible intervals. Circles represent individual trees with (1) or without (0) hollows.

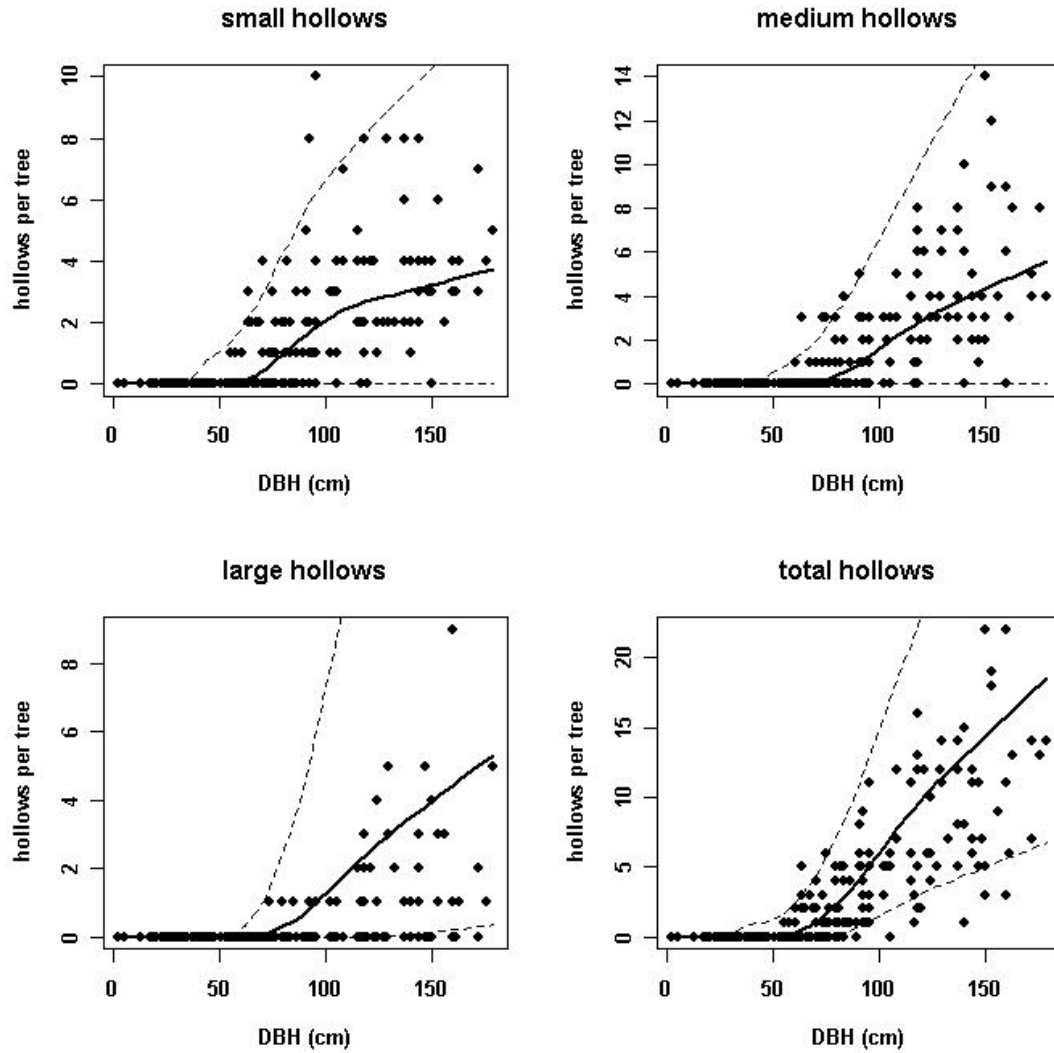


Figure 4. Relationship between tree size (DBH) and number of hollows in each of three size classes (small = < 5 cm diameter hole, medium = 5 < diameter < 15, large = diameter > 15 cm) and total number of hollows. Solid lines are posterior means from Poisson regression, dashed lines 95% credible intervals.

### ***Estimated density of hollow-bearing trees in Barmah forest***

We used the fitted relationships between probability of hollows and tree size to estimate the expected number of hollow-bearing trees (HBT) in each CFI plot at each measurement date (Table 4, Figures 5, 6). Assuming the CFI plots collectively are representative of size class distributions and stem densities across Barmah forest, these results, together with direct measurements (Table 4), suggest that the average density of hollow-bearing trees across Barmah forest (i.e. excluding swamps and open grasslands) is in the order of 15 trees per ha (Table 4, Figures 5, 6). The HBT density estimated from CFI size class distributions and model relationships between DBH and hollows is consistent with the average density of hollow-bearing trees observed by Bennett et al. (1994) at Barmah forest (15 HBT ha<sup>-1</sup> red gum dominated sites, and 28 HBT ha<sup>-1</sup> in box-dominated sites), with Newton John's (1992) data from 7 sites (15.5 - 21.7 HBTs ha<sup>-1</sup>), and with our own observations in randomly selected sites (17 HBTs ha<sup>-1</sup>). Lumsden et al. (2002) reported a mean density of HBTs across 58 1-ha sites at Barmah forest of 10.5 (SD = 5.9) and the mean density of live HBTs to be just 6.1 (SD = 5.5). However, the sites of

Lumsden et al. (2002) were selected randomly from a grid of the study area that included swamp and open grassland sites that inevitably have few, if any, hollow-bearing trees. The area from which sites were selected (within 13 km of capture sites in adjacent farmland) also included proportionately more areas of regrowth than Barmah forest in general.

Based on the average number of hollows per tree (10.5, Lumsden et al. 2002), we estimate the average density of hollows to be ca 100 hollows ha<sup>-1</sup>. This value is consistent with Newton-John's (1992) estimated average of 92 "useable hollows" per hectare in Barmah. Newton-John's estimate was based on a total sample of 158 trees over 7 sites, of which 70 trees had hollows (average 6.0 hollows per hollow-bearing tree). Harper et al. (2004) found that ground surveys underestimate the actual number of hollows by at least 50% (i.e. less than half of all hollows are visible from the ground), in which case the actual density of hollows in Barmah forest could be closer to 200 hollows per ha.

There is considerable spatial variation in the density of hollow-bearing trees (Figures 5, 6), reflecting the mosaic of forest age-structures and disturbance histories, but all plots were observed (2007 plots) or predicted (CFI) to include some hollow-bearing trees (minimum observed density = 2.0 ha<sup>-1</sup>, minimum predicted density in 2006 CFI = 1.2 ha<sup>-1</sup>). Regrowth areas clearly will have very few HBTs, but such stands make up < 3% of SFRI classified forest in Barmah forest (Figure 2, Table 1).

Based on size-class distributions in CFI plots, the density of hollow-bearing trees likely has remained relatively stable over the past 40 years (Figure 5-7). The average predicted density of hollow-bearing trees calculated for CFI plots in 2006 is lower than calculated averages for earlier years (Table 4). However, only 29 of 55 CFI plots were surveyed in 2006, and those plots underestimate the average density in all CFI plots in each year prior to 2006. When data from plots that were not surveyed in 2006 was excluded from calculations for all years there was little evidence of a declining trend (Table 4). The average density of hollow-bearing trees in the two randomly selected plots that we sampled in 2007 was similar to the CFI average for 1995 (Table 4). There appears to have been an increase in densities of trees 25 cm < DBH < 50 cm after 1979 at many CFI plots (Figure 7), which is reflected in lower median DBH for all trees (Figure 7). This suggests the potential for increases in HBT densities in these plots over the next 50+ years if those trees continue to grow and the majority of existing trees > 50 cm DBH are retained.

**Table 1. Extent of SFRI forest stand attributes (a) relative age and (b) crown size in Barmah forest and number of CFI and 2007 plots falling within stands of each classification.**

	Extent in Barmah		2006 CFI plots		2007 plots	
	hectares	% of total	number	% of total	number	% of total
(a) Relative stand age						
Senescent	146.6	0.5	0	0	0	0
Late Mature	1027.1	3.8	2	6.9	1	7.6
Mature	17776.5	65.0	17	58.6	7	54.0
Uneven	7611.4	27.8	10	34.5	3	23.0
Regrowth	802.4	2.9	0	0	2*	15.4
Total	27364.1		29		13	
(b) Crown size (m)						
<5	1817.9	6.7	2	6.9	1	7.6
5-9.9	12532.0	45.9	16	55.2	3	23.1
10-14.9	12378.6	45.3	9	31.0	0	0
15-19.9	600.8	2.2	2	6.9	9	69.2
Total	27364.1		29		13	

Historical densities of hollow-bearing trees are extremely difficult to estimate, but there is little doubt that floodplain forests in the 19<sup>th</sup> century had a much older age-structure than those of

today (Mac Nally and Parkinson 2005). Historical records (cited in Mac Nally and Parkinson 2005) suggest densities of large trees - usually defined as suitable for milling, or > 2 feet (> 61 cm) in diameter - ranging from 15 to 50 trees per hectare in Murray floodplain forests in the late 19<sup>th</sup> century. One area near Moira was estimated to have 80–100 large (18–24 inches [45–60 cm] in diameter) trees per acre (0.4 ha), equivalent to > 200 large trees ha<sup>-1</sup>. The average density of hollow-bearing trees in Barmah forest is, therefore, at the low end of historical values for red gum floodplains, and densities of very large, old trees, which provide many hollows of all size classes, are almost certainly lower than prior to European settlement. Fallen timber loads are also thought to be lower than pre-European levels according to Mac Nally and Parkinson (2005) who estimated 24 tonnes ha<sup>-1</sup> in Barmah, the highest of all red gum forests surveyed, but possibly only ~ 25% of pre-European levels.

Bennett et al. (1994) found that HBT densities across a range of northern plains (Victoria) woodland types generally were lower in large blocks of public land subject to timber harvesting than in smaller, private blocks with less harvesting. While this pattern holds for river red gum forests, HBT densities within red gum sites were higher in Barmah forest (3 sites, mean 15.5 ha<sup>-1</sup>) than in other large (>200 ha), public blocks (mean  $\pm$  SD =  $8 \pm 7$ ), and only marginally lower than in small (<40 ha), private blocks ( $20 \pm 11$ ). This suggests that either harvesting may not have depleted HBTs in Barmah forest as much as in other areas, or that densities were initially higher in Barmah. Barmah forest represents a particularly important habitat for hollow-dependent fauna in the northern plains.

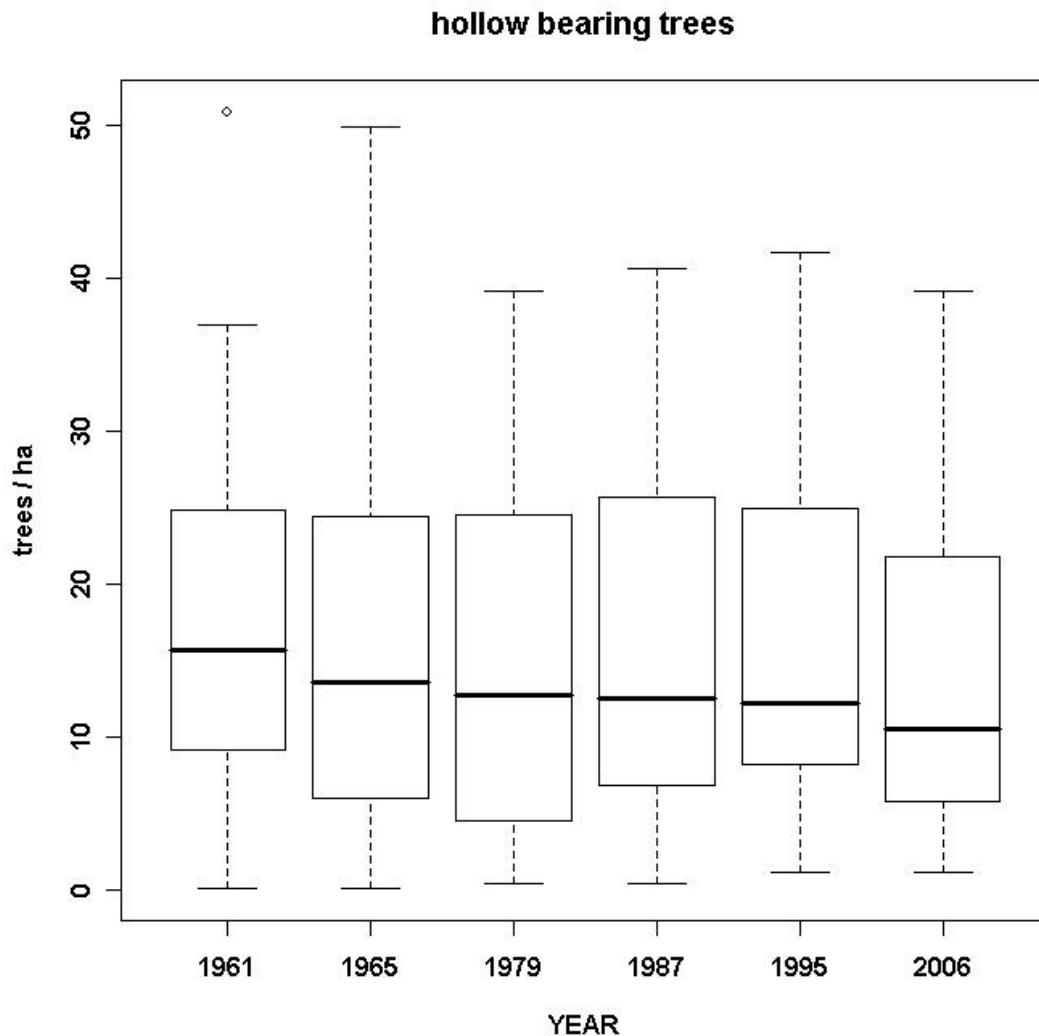




Figure 5. Estimated numbers of hollow-bearing trees per hectare in CFI plots in each year of measurement. Boxes indicate the median (bold line) and 25<sup>th</sup> to 75<sup>th</sup> quantiles. Whiskers extend to 1.5 times the interquartile range. Circles indicate outliers. Sample sizes are 53, 53, 52, 55, 55 and 29 plots for 1961 through 2006. HBT densities were estimated by applying fitted Bayesian logistic regression models (Model 1) to data for each tree to derive a posterior probability that the tree contained at least hollow of a particular size. The estimated number of trees with hollows in each size class in each plot class was then estimated as the summed probabilities for all trees in the plot. These values were summed to obtain expected totals. Estimations were performed in WinBUGS simultaneously with model fitting and therefore are based on the full joint posterior distributions of model parameters. That is, parameter uncertainties are reflected in the estimates of HBTs densities.

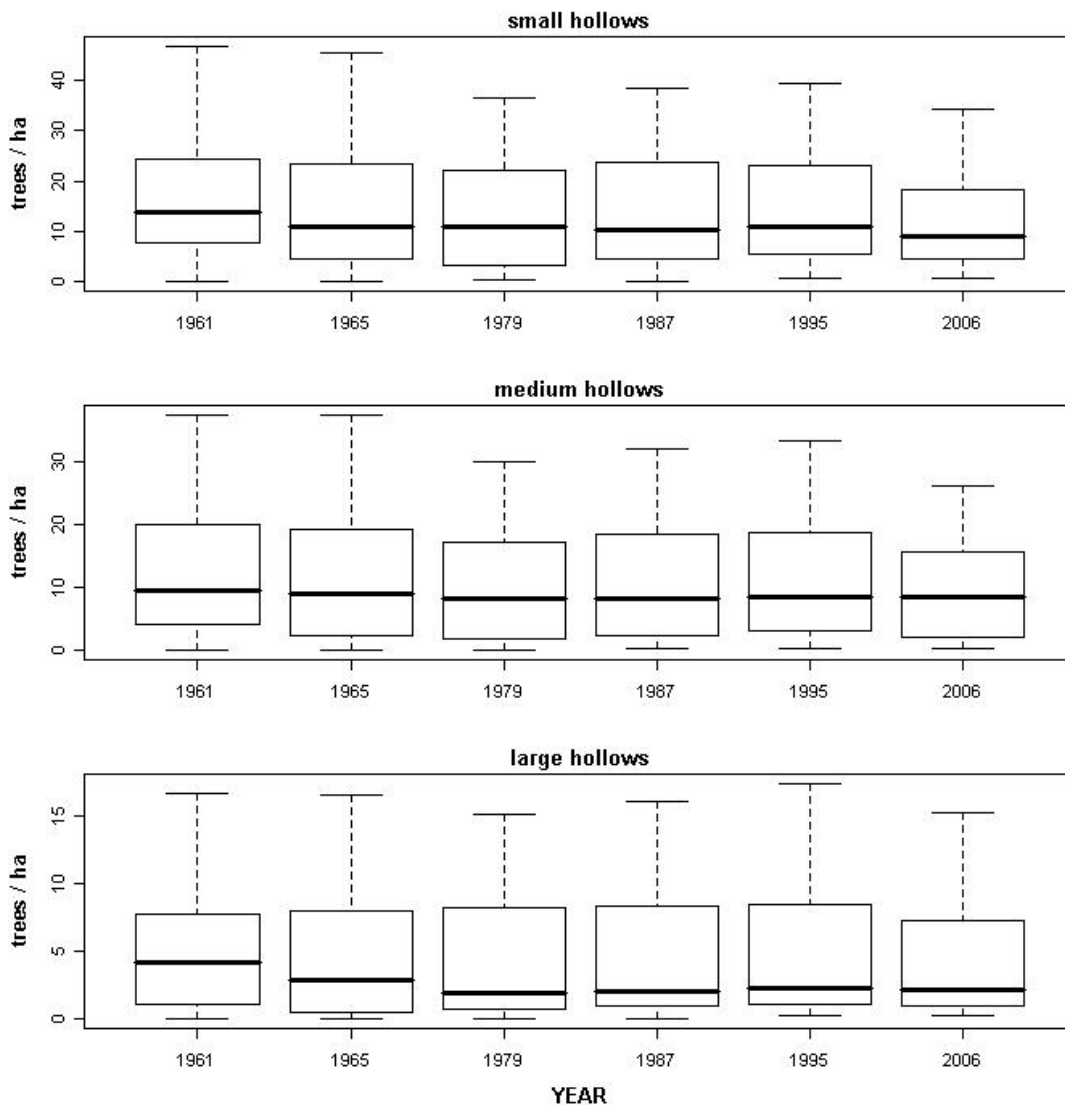


Figure 6. Estimated densities of trees bearing hollows in each size class in CFI plots in each year of measurement. Estimation methods, plot formats and sample sizes as for Figure 5.

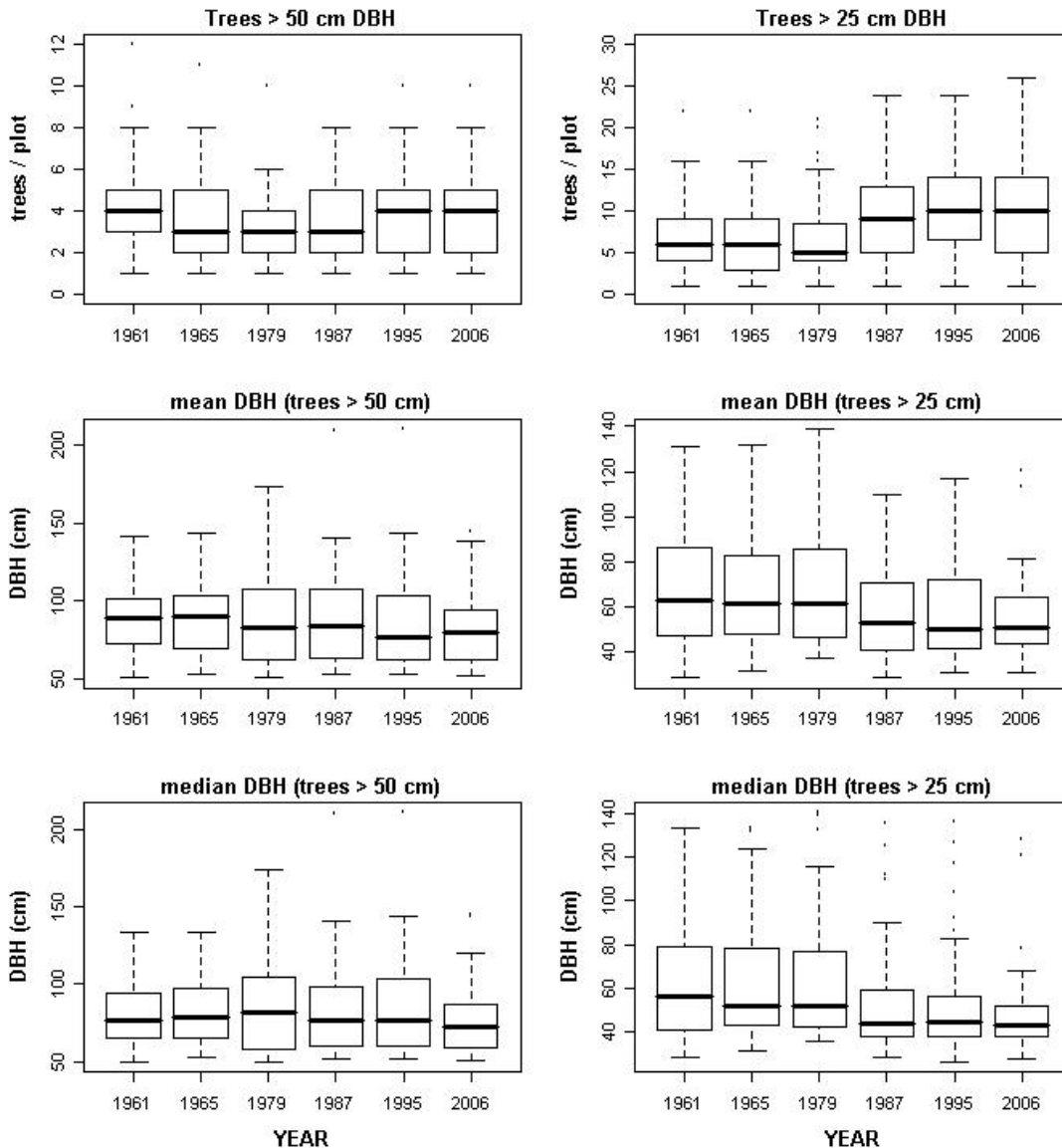


Figure 7. Variation in densities and mean and median diameters at breast height (DBH) for all trees > 50 (Left hand plots) or > 25 (right hand plots) DBH in CFI plots. Boxplots and sample sizes as for Figure 5.

### ***River red gum growth rates and future provision of hollows***

Growth rates of river red gum appear to have declined in the last decade, almost certainly due to reduced frequency of flooding, decreased rainfall and falling water tables. The Victorian Environmental Assessment Council (VEAC 2007) estimated mean diameter growth rates of just  $0.19 \text{ cm yr}^{-1}$  in the period 1987 to 1995, compared with an average rate of  $0.39 \text{ cm yr}^{-1}$  over the previous four decades. Our modeling of CFI data shows that growth rates decline with increasing stem densities and with lower mean water table depths (a surrogate for water availability) (Table 5, Figure 8). The estimated density effect was stronger than the groundwater effect, but fewer data were available for the latter. Future effort should incorporate better estimates of hydrological conditions, including improved groundwater modeling and estimates of inundation frequencies. Some of this work is being undertaken as part of ongoing river red gum health studies (VEAC 2007, S. C. Cunningham pers. comm.).

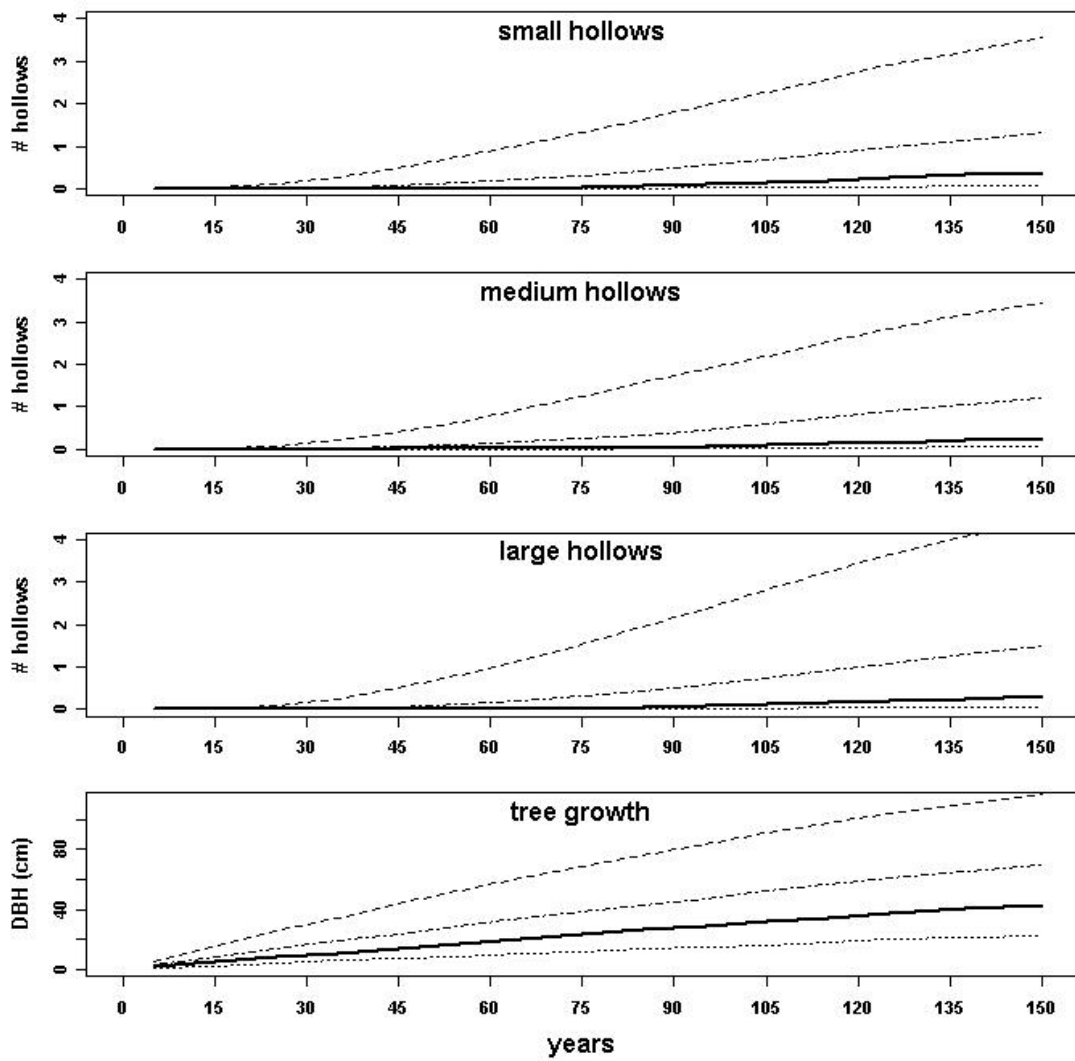


Figure 8. Modelled growth rates (bottom plot) and resulting provision of small (top), medium and large hollows for individual trees through time. Solid lines are posterior means, dashed lines 95% credible intervals.

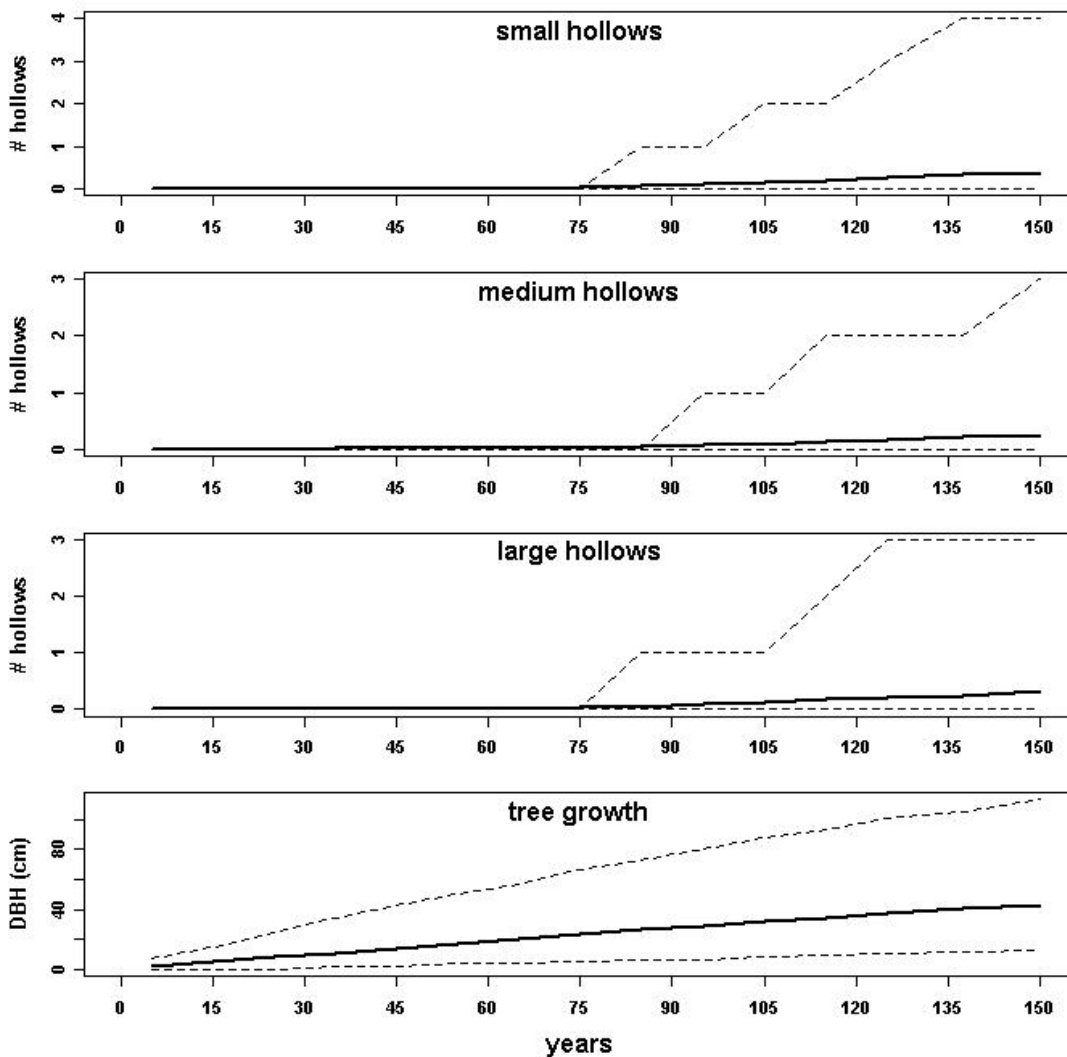


Figure 9. Modelled growth rates (bottom plot) and resulting provision of small (top), medium and large hollows for individual trees through time. Solid lines are posterior means, dashed lines 95% credible intervals.

Simulations based on the growth model that incorporate variability in growth rates among trees and plots, and parameter uncertainty, suggest an absolute minimum age of 75 years before any trees would produce hollows under average growth conditions, but the average number of hollows per tree would remain  $< 1$  beyond 150 years. That is, based on the average growth rates experienced since 1961 it would take  $> 150$  years for a tree planted now to reach hollow-bearing size (50 cm DBH).

In Figures 10 and 11, we present estimated proportions and densities of HBTs, respectively, under four sets of growth conditions: low density, high water table; average density, average water table; high density, low water table; and low density, low water table. These estimates were derived from model 3 using the joint posterior distributions of parameters conditioned on CFI data.

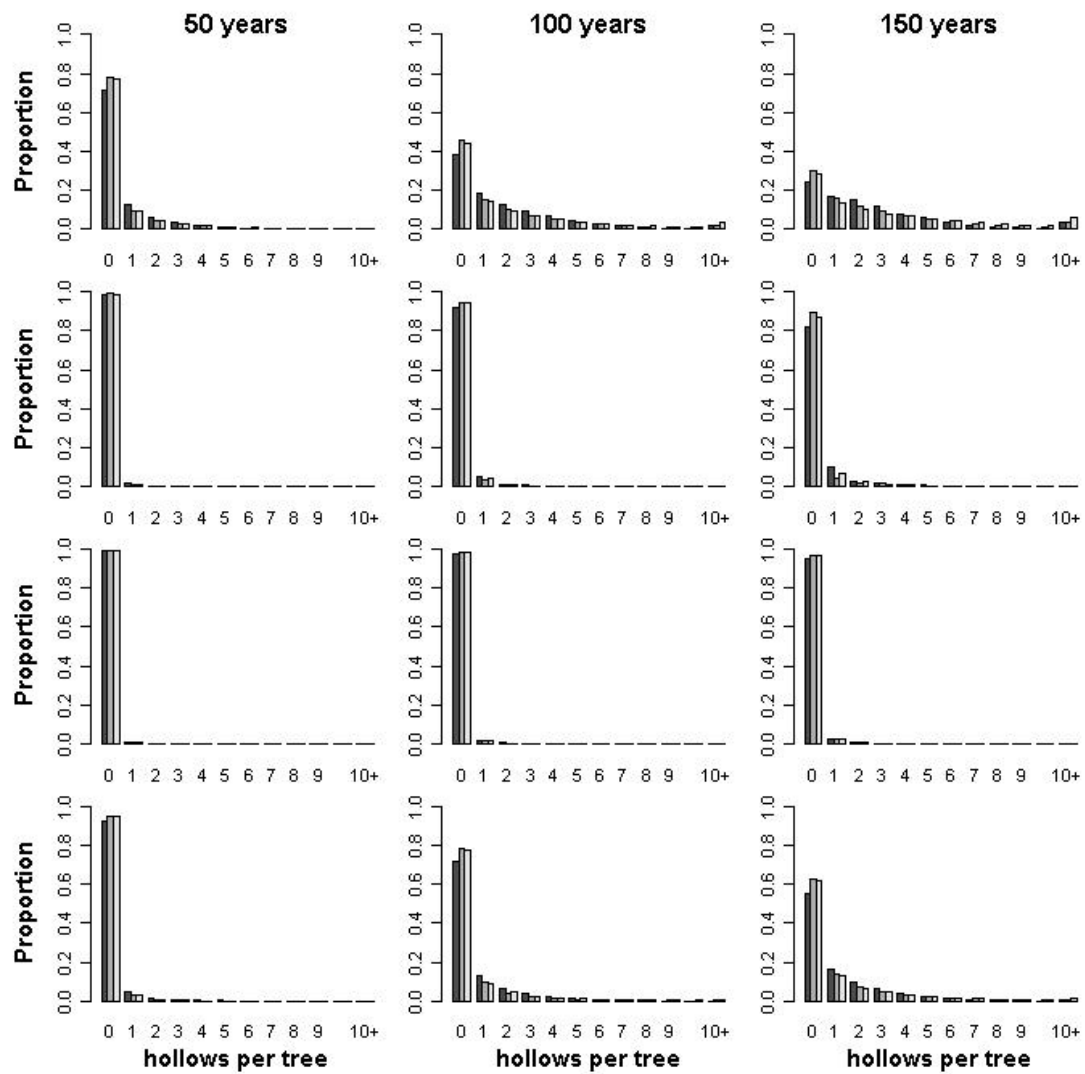


Figure 10. Proportion of trees expected to have hollows after 50, 100 and 150 years under four sets of growth conditions: 1<sup>st</sup> row (top) = low density, high water table (top), 2<sup>nd</sup> row = average density, average water table, 3<sup>rd</sup> row = high density, 4<sup>th</sup> row (bottom) = low density, low water table. Darkest bars are small hollows, lightest bars large hollows.



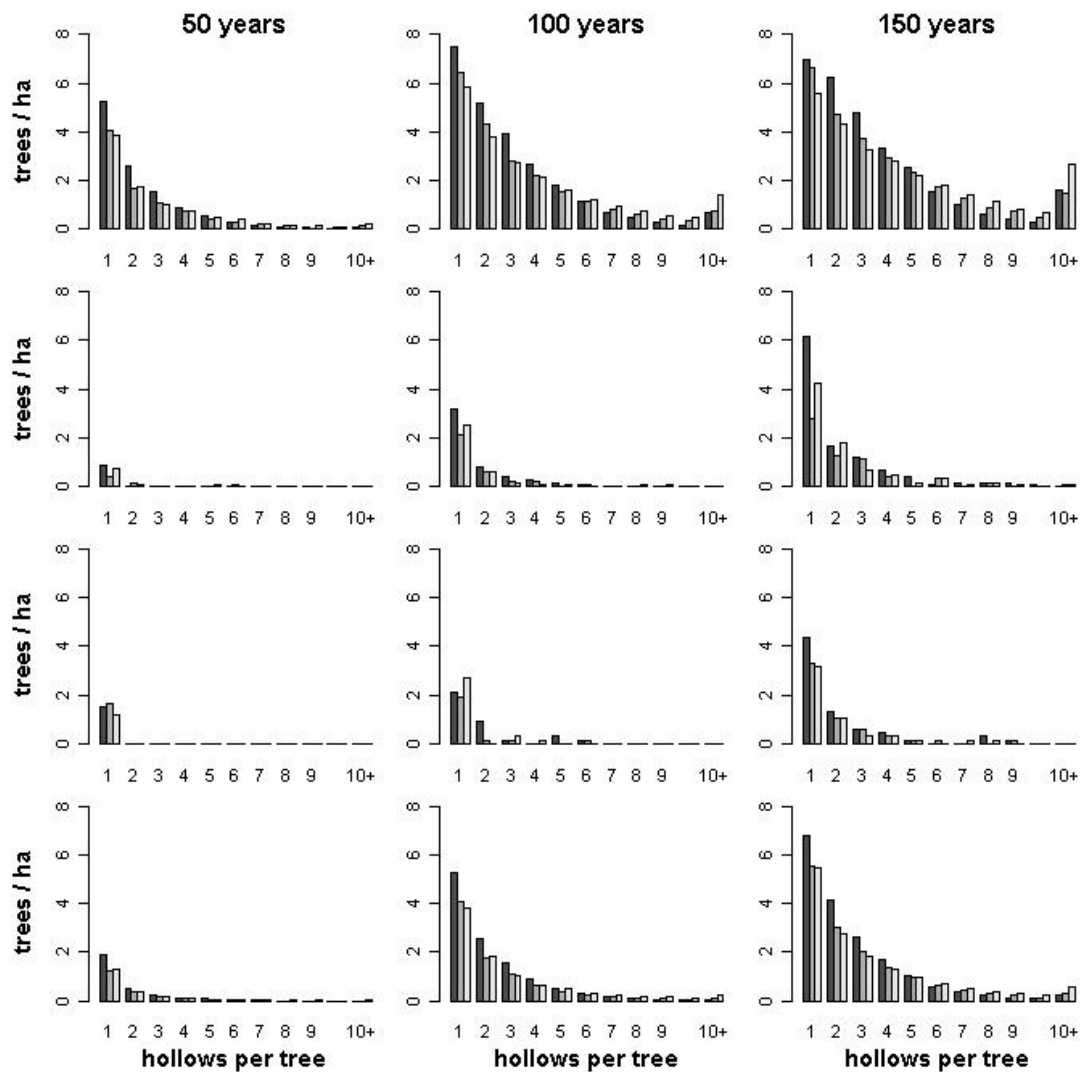


Figure 11. Expected density of hollow bearing trees (by number of hollows per tree) under four sets of growth conditions: 1<sup>st</sup> row (top) = low density, high water table (top), 2<sup>nd</sup> row = average density, average water table, 3<sup>rd</sup> row = high density, 4<sup>th</sup> row (bottom) = low density, low water table. Darkest bars are small hollows, lightest bars large hollows.

The results show how density and ground water levels affect growth rates, and therefore rates of hollow provision in red gums. Assuming average conditions (densities and water table levels) achieving current densities of hollow bearing trees from regeneration alone would take > 150 years. Even under very good growing conditions (low density, high water table) it would take > 100 years to replace existing hollow-bearing trees. Maintaining low densities would increase the rate of hollow provision; 40 trees ha<sup>-1</sup> is predicted to produce more hollow-bearing trees in 100 and 150 years under current hydrologic conditions than 60 or 120 trees ha<sup>-1</sup> under the same conditions. This suggests that ecological thinning and or selective harvesting may be required to maintain tree growth in some areas if declines in water availability are not reversed.

The overwhelming conclusion from these simulations is that it is essential to protect existing hollow-bearing trees and sufficient trees in smaller size classes to maintain a continual supply of hollow-bearing trees into the future. Given the very slow growth rates of river red gum it may take >100 years for trees to reach sufficient size to develop habitat hollows, even under good growing

conditions. As flooding become less frequent and water tables drop, growth rates will continue to decline, making it even more difficult to “replace” hollow-bearing trees through regeneration or planting. Therefore, it is critical to retain not only existing hollow-bearing trees, but also trees that will provide hollows in the decades to come. Long-term sustainability requires a management system that maintains all sizes classes of trees and ensures adequate retention of young trees for recruitment as habitat trees.

Current forestry code of practice for mid-Murray prescribe the mandatory retention of all trees in which threatened species are known to nest, all trees > 100 cm DBH, and a minimum 20 trees per 10 ha of size 50 cm < DBH < 100 cm (DSE 2007b). These prescriptions probably would maintain current densities of hollow-bearing trees in the medium term (decades) if mortality rates were low. River red gums may live for 400+ years (L. Bren, unpublished), so there is potential for individual trees to provide habitat hollows for centuries, even if it takes > 150 years for hollows to develop. However, reduction in flooding frequency has severely stressed river red gums in Murray floodplains and mortality rates are likely to increase. In 2004 the Murray Darling Basin Commission (MDBC 2003) reported that the condition of trees in the lower Murray were in steady decline, with 75% of red gums “stressed”, “near dead” or “dead”. Cunningham et al. (2007) found that only 22% of Barmah forest was in good condition in 2006. Without increased water, a large proportion of the hollow-bearing trees in Barmah forest will die. Senescing and dead trees provide hollows, but not as many as healthy, large old trees (Newton 1992) and only for relatively short periods. The declining frequency of flooding flows in Barmah forest and other floodplain forests threatens the very existence of those forests. The subsequent loss of nesting and roosting habitat for at least 60 vertebrate species would be just one of many dire consequences for biodiversity in northern Victoria.

Unsustainable timber harvesting remains a potential threat to the long term provision of hollows in Barmah. Excessive harvesting of trees < 50 cm DBH would reduce the long term recruitment of habitat trees and lead to an eventual decline in such trees as older trees senesce. Current management prescriptions do not provide for the retention of habitat trees < 50 cm DBH, so it is possible that most or all trees < 50 cm could be removed from harvested areas over several harvesting cycles, especially if licensed volumes exceed sustainable levels. The draft VEAC River Red Gum Investigation report (VEAC 2007) estimates that without delivery of significant environmental flows (ca 900 GL every 5 years for Barmah) timber yields in Barmah and Gunbower forests will decline to ~61% of current volumes. It is critical that sustainable yields be carefully calculated to account for changing hydrologic conditions. Unsustainable harvesting will threaten long term recruitment of hollow-bearing trees.

Some timber harvesting is not necessarily incompatible with the long-term provision of hollows (and other habitat resources) within Barmah. The selective logging practices employed at Barmah forest facilitate retention of scattered future and present habitat trees and the tall straight trees with small branches that are favoured for timber harvesting may be less valuable as future habitat trees than trees with spreading or irregular crowns. By reducing stem densities, selective logging may also reduce competition so that retained habitat trees reach hollow-bearing size classes more rapidly. However, harvesting must be carefully managed. Sustainable yields must be calculated based on expected hydrological conditions and must account for the need to retain habitat trees in all size classes. Furthermore, restrictions must be enforced strongly, and the impacts of harvesting operations on retained trees and other habitats should be monitored. There are concerns that harvesting operations increase mortality and damage to retained trees (Gibbons and Lindenmayer 2002, VEAC 2007), and contribute to soil disturbance and dispersal of weeds (VEAC 2007). Recent suggestions that trees > 100 cm DBH have been harvested (VEAC 2007) is cause for concern.

***Is the number of hollow-bearing trees in Barmah forest limiting populations of hollow-dependent fauna?***

Given large variation in the number, size and quality of hollows among trees of a given size, and the paucity of data on species preferences for hollow characteristics, estimating the total density of hollows available to particular species is extremely difficult. Equally, there are few reliable

estimates of the densities of hollows or hollow-bearing trees required to sustain viable populations of hollow-dependent species, and the data requirements for building such models are extensive. Data on distributions and densities of hollow-dependent fauna in Barmah forest are inadequate for quantitative assessments of population viability.

Some studies have estimated the density of hollow bearing trees that are used by fauna ( $H$ ) with the simple formula (Gibbons and Lindenmayer 2002):

$$H = \sum_{n=1}^N \frac{D_n I_n}{T_n} \quad \text{equation 1}$$

Here  $N$  is the number of hollow-dependent species,  $D_n$  is the density of species  $s$ ,  $I_n$  is the number of hollows required by individuals of species  $s$ , and  $T_n$  is the average number of suitable hollows per tree. Smith et al. (1994) estimated that a total density of 6–13 hollow-bearing trees  $\text{ha}^{-1}$  were used by 70 hollow-dependent species (20 bats, 12 arboreal mammals, 26 birds and 14 reptiles) in north-east NSW. Gibbons (1999) estimated 7–14 HBTs  $\text{ha}^{-1}$  would be used by 46 vertebrate species in East Gippsland, and Lamb et al. (1998) estimate that 4.5–9 HBTs  $\text{ha}^{-1}$  would be used by 95 vertebrate species in south-east Queensland. Fifty-eight species that are dependent (39) on or use (19) hollows inhabit or have been recorded in Barmah, including 36 birds, 12 bats, 7 arboreal mammals, and 3 reptiles (Table 2). Four of these are vagrant species that would have little impact on hollow availability, and several others occur in very low densities. Data on species densities ( $D_n$ ) and hollow requirements ( $I_n$ ) are lacking for most of these species. However, present densities of HBTs in Barmah forest are at the upper end of estimated requirements for similar or more specious hollow-dependent fauna in other forest types.

### Birds

Numerically, birds are the dominant users of hollows in Barmah, both in terms of species and individuals. Hollow-nesting birds comprise 30 – 50% of all individual land birds in mature river red gum and box sites (Loyn et al. 2002). Loyn et al. (2002) reported a mean density of hollow-nesting birds in Barmah forest of 23.5 individuals  $\text{ha}^{-1}$  in 1978 (94 individuals per 4 ha site observed in 1 hr). Maximum counts (over 8 surveys) equate to densities ranging from 6.5 to 29.5 hollow-nesting birds  $\text{ha}^{-1}$  at seven 2 ha sites surveyed by Mac Nally et al. (2001) in 2000, but the average density recorded over 8 surveys was just 4.7 individuals  $\text{ha}^{-1}$ . If birds use one hollow per breeding pair (a reasonable assumption for most birds) and there was on average only one suitable hollow per hollow-bearing tree (a conservative figure given that we and Newton-John (1992) found on average 6 *visible* hollows per hollow-bearing tree), equation 1 implies that the density of hollow-bearing trees used by birds would range from 2.3 to 15  $\text{ha}^{-1}$  (depending on the bird density estimate used).

Brown Treecreepers (*Climacteris picumnus*) were among the three most abundant bird species recorded at Barmah forest by Chesterfield et al. (1984) in the late 1970s and by Mac Nally et al. (2001) in 2000. Cooper (2000) found that the presence, fitness and density of Brown Treecreepers was influenced by the density of hollows in New England Tablelands. In one study, Cooper found low probability of occurrence when hollow densities were  $< 40 \text{ ha}^{-1}$ . In a separate study, the most productive territories had  $> 50$  hollows  $\text{ha}^{-1}$  but territories with  $< 40$  hollows  $\text{ha}^{-1}$  also supported successful breeding groups, indicating that areas with  $< 40$   $\text{ha}^{-1}$  may still be viable habitat. We estimate that hollow densities  $> 40 \text{ ha}^{-1}$  across most of Barmah. Declines in populations of the Brown Treecreeper have been linked to fragmentation and reduced foraging habitat, specifically the disruption of female dispersal among isolated habitats (Cooper 2000). Mac Nally (2006) found sustained increases in Brown Treecreeper densities following experimental increases in fallen timber loads at Gunbower forest, where densities of HBTs seem to be lower than at Barmah. Such positive responses to increases in foraging substrates would be unlikely if populations were limited by the availability of hollows. While increased local densities do not necessarily translate to increased populations sizes, breeding success is positively associated with group size.

In 2002, the Department of Sustainability and Environment reported 16 known breeding sites of the Superb Parrot (*Polytelis swainsonii*) in Barmah. These sites are special protection zones. Nests typically occur in healthy large, old, river red gums with multiple spouts, but also occur in dead trees. The loss of box woodland foraging habitat close to suitable breeding sites is a major reason for the threatened status of this species.

Some of the more prominent hollow users are owls which utilize a variety of cavities for both nesting and diurnal roosting. Of the four owl species recorded from the Barmah forest area, Southern Boobook (*Ninox novaeseelandiae*), Barn Owl (*Tyto alba*), Barking Owl and Australian Owlet-nightjar (*Aegotheles cristatus*), the Barking Owl is regarded as endangered. Another endangered species, the Powerful Owl has been recorded further east along the Murray River in similar River Red Gum habitat and is likely to be intermittently present given its large foraging range (DSE 2007a). Given the apparent suitable range of hollows available in Barmah forest the limiting factor for the larger owls is likely to be low numbers of ground mammals that are in turn probably limited by habitat availability (i.e. fallen timber). Incidental observations of Southern Boobooks increased around experimentally increased fallen timber sites on Gunbower Island containing increased populations of antechinus (G. F. B. Horrocks, pers obs.).

#### *Terrestrial and Arboreal Mammals*

Barmah forest has a depauperate small mammal fauna with only arboreal and semi-arboreal species persisting (Loyn et al. 2002). This may be a natural consequence of the (once) regular flooding regimes, but there is evidence that terrestrial mammals have suffered from European settlement. Grazing and trampling by feral animals has altered the floral composition, fallen timber cover has been systematically removed and predation by introduced species has had a negative impact on mammal populations throughout the region.

The most abundant small ground mammal is the Yellow-footed Antechinus (*Antechinus flavipes*). Antechinus forage both on trees and on the ground using cavities in both trees and fallen timber to nest and shelter. Lada et al. (2007) surveyed antechinus populations at several sites across south-eastern Australia, including Barmah and Millewa forests. The highest density recorded in Barmah forest over 4 years was 2.4 individuals ha<sup>-1</sup>. This density is much lower than in nearby Millewa forest, 4.1 ha<sup>-1</sup> and other northern plains sites. The average density of trees > 60 cm DBH at surveyed areas was 17.4 ha<sup>-1</sup> at Barmah forest and 13.5 ha<sup>-1</sup> at Millewa. Assuming similar size class distributions at these sites as in Barmah forest CFI plots, these tree densities would equate to approximate densities of hollow-bearing trees of 13 ha<sup>-1</sup> and 10 ha<sup>-1</sup> for Barmah and Millewa forests, respectively (not including trees < 60 cm DBH, some of which would be expected to provide hollows). The fact that antechinus are more abundant at Millewa forest than at Barmah forest, but large trees (> 60 cm DBH, therefore high probability of being hollow-bearing) are more abundant at Barmah suggest that antechinus are not limited by the availability of hollows in these forests. Antechinus populations increase following floods (Lada et al. 2007), probably because of increased productivity of floodplain invertebrates (Ballinger et al. 2005). Antechinus densities also increase with increasing fallen timber, which provides substrate and cover for foraging animals (Mac Nally and Horrocks 2002, Lada et al. 2007).

The Squirrel Glider (*Petaurus norfolcensis*) and Brush-tailed Phascogale (*Phascogale tapoatafa*) only rarely have been reported at Barmah forest (Loyn et al. 2002) although the gliders can be found in good numbers further east along the Ovens River. Brush-tailed Phascogales are more usually found in dry woodland particularly Box-Ironbark and the Barmah forest is highly unlikely to be an important site for this species. Squirrel gliders have been recorded in River Red Gum forest but the lack of suitable understorey cover is likely to restrict their occurrence in Barmah. Both species require multiple hollows as they are known to rotate their den sites (Menkhurst 1995) and the lack of coarse woody debris would have a negative impact on the phascogale.

#### *Bats*

All but one species of insectivorous bat known from the northern plains occurs in Barmah. Most species are dependent on hollows and fissures in large old trees for roosting. The only threatened

bat species recorded from Barmah forest was the southern form of the Large-footed Myotis (*Myotis adversus*, DSE 2003). This water foraging species generally roosts in caves but is known to use hollows close to riparian areas.

In a study at Barmah forest, Lumsden et al. (2002) found that while radio-tracked Lesser-longeared Bats (*Nyctophilus geoffroyi*) and Gould's Wattled Bats (*Chalinolobus gouldii*) foraged in remnant vegetation within the rural landscape, females of both species roosted in large old or dead river red gums within the forest itself. Individuals apparently travel long distances from foraging areas in farmland to roosting sites within Barmah. Individual bats are known to use more than one roost site over time to both avoid predators and to promote hygiene.

### *Reptiles*

River red gum forests generally have low reptile diversity even in areas of high habitat resources (DSE 2007a). Carpet Pythons (*Morelia spilota metcalfei*) and Lace Monitors (*Varanus varius*) require hollows as den sites and to provide habitat for their major prey items. While known to forage on the ground they are less dependent on fallen timber than some of the other more common skinks found in these floodplain forests. The gradual decline in the number of these two significant species is likely to be a reflection of the continual destruction and fragmentation of suitable habitat, illegal collection and predation by introduced animals rather than the lack of suitable hollows.

### *Summary*

Among both bird and small mammal assemblages, obligate ground feeders are scarce or absent from much of Barmah, whereas species that forage on trees (bark gleaners, nectarivores) and aerial insectivores (bats) are common, or at least still present. Hollow availability is necessary but not necessarily sufficient to maintain populations of hollow-dependent fauna. The hollow-dependent species that are rare in Barmah forest are those whose prey or foraging grounds appear to have been depleted. As Loyn et al. (2002) suggested "perhaps the deduced loss of mammal species from Barmah forest owes more to the loss of adjacent woodlands, than to changes within the forest itself". Bird and mammals that nest in hollows and forage in trees, or in aquatic habitats, generally are abundant at Barmah forest. Obligate ground foraging mammals, birds and reptiles are rare or absent, regardless of nesting habitats.



## **Conclusions**

Reduced densities of large hollow-bearing trees almost certainly increased pressure on populations of hollow-dependent fauna following European settlement of Murray River floodplains. However, the relative contribution of the reduction in hollow-bearing trees to population declines and species diversity is unclear. Altered flow regimes, land clearing, grazing, timber harvesting, altered fire regimes, and introduced species have affected the productivity of floodplain habitats, depleted adjacent woodland foraging habitats, and increased direct mortality of many species. None of the vertebrate species that have apparently disappeared from Barmah forest (or the northern plains in general) since European settlement are hollow dependent (Loyn et al. 2002). There is little available evidence that hollows presently are a limiting resource for any populations in the region. However, the paucity of data makes a proper assessment of the adequacy of the resource extremely difficult. Detailed faunal surveys and manipulations of hollow densities are required before firm conclusions can be made. The biggest threat to all fauna within red gum forests is continued declines in red gum health and floodplain productivity caused by river regulation, water extraction and drought. This also is exacerbated by selective harvesting of trees < 50 cm DBH, which prevents them progressing eventually into the size-classes at which hollows develop.

## **Recommendations**

### *Resource management*

- (1) Environmental flows are critical as is groundwater availability
- (2) Sustainable timber yields must be re-evaluated to account for declining growth rates
- (3) Retention of trees in all size-class should be mandated to ensure continual recruitment of trees to hollow-bearing cohorts.

### *Further research (field based and modeling) is required to determine*

- (4) Impacts of harvesting operations on health of retained habitat trees in Barmah
- (5) Impacts of ecological thinning on growth rates and size-class distributions under changing water regimes.
- (6) Quantitative surveys of hollow-dependent fauna and detailed studies of hollow occupancy and availability are required to establish the extent of competition for hollows and the relative importance of this in limiting or threatening current populations.

Faunal surveys conducted now would also help in assessment of the ecological responses to future management, such as further restrictions on grazing, timber harvesting, environmental flows, and pest control. The complexities of managing floodplain ecosystems subject to multiple past and present natural and anthropogenic disturbances require an adaptive management approach, which in turn requires baseline data and ongoing monitoring. Monitoring programs have been implemented for a range of flora and fauna with Barmah forest as part of the living Murray initiative (MDBC 2007) but hollow-dependent fauna are poorly targeted. This is a concern given that Barmah forest is a major habitat for many hollow-nesting species, including 15 species thought to be under some threat (DSE 2003, DEC 2007), and the loss of habitat hollows is often cited as a contributing factor to biodiversity in the region.

## **Consultations**

In the course of our investigation information regarding red gum hollows, with particular reference to the Barmah forests, was provided by the following

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## References

- Alexander J.S.A, Scotts D.J. and Loyn, R.H. (2002) Impacts of timber harvesting on mammals, reptiles and nocturnal birds in native hardwood forests of East Gippsland, Victoria: a retrospective approach. *Australian Forestry* **65**, 182-210.
- Ambrose, G. J. (1979) An ecological and behavioural study of vertebrates using hollows in eucalypt branches. PhD thesis, La Trobe University, Melbourne.
- Barrett, G., A. Silcocks, S. Barry, R. Cunningham, and R. Poulter. 2003. The New Atlas of Australian Birds. Birds Australia. Birds Australia (Royal Australasian Ornithologists Union), Melbourne.
- Ballinger, A., Mac Nally, R., Lake, P.S., 2005. Immediate and longer term effects of managed flooding on floodplain invertebrate assemblages in south-eastern Australia: generation and maintenance of a mosaic landscape. *Freshwater Biology* **50**, 1190–1205.
- Bennett, A.F., Lumsden, L.F. and Nicholls A.O. (1994) Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. *Pacific Conservation Biology* **1**, 222-235.
- Beyer, G.L. and Goldingay, R.L. (2006) The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. *Wildlife Research* **33**, 161-174.
- Cameron, M. (2006) Nesting habitat of the Glossy Black-cockatoo in central New South Wales. *Biological Conservation* **127**, 402-410.
- Chesterfield, E. A., Macfarlane, M.A. and Loyn, R.A. (1984) Flora and Fauna of Barmah State Forest in relation to Management unpublished report to Forest Commission of Victoria.
- Cockburn, A. C. and Lazenby-Coben, K. (1992) Use of nest trees by *Antechinus stuartii*, a semelparous lekking marsupial. *Journal of Zoology* **226**:657-680
- Cooper, C. B. (2000) The behavioural ecology and conservation of an Australian passerine the Brown Treecreeper *Climacteris picumnus* PhD Thesis Faculty of Virginia Polytechnic Institute and State University
- Cressie, N. A. C. 1993. Statistics for spatial data. Wiley, New York.
- Cunningham, S. C., Mac Nally, R. White, M., Read, J., Baker, P.J., Thomson, J. and Griffioen, P. (2007) Mapping the Current Condition of River Red Gum (*Eucalyptus camaldulensis* dehn.) Stands Along the Victorian Murray River Floodplain. A Report to the Northern Victorian Catchment Management Authorities and the Department of Sustainability and Environment. Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Melbourne.
- Dickman, C. (1991) Use of trees by ground-dwelling mammals: implications for management. In 'Conservation of Australia's forest fauna'. (Ed. D Lunney) pp. 125-136. (Royal Zoological Society of New South Wales: Sydney)
- DEC (Department of Environment and Conservation NSW (2007) Threatened Species website
- DNRE (Department of Natural Resources and Environment) 2002 Threatened Vertebrate Fauna in Victoria 2000 : A systematic list of vertebrate fauna considered extinct, at risk of extinction or in major decline in Victoria DNRE: East Melbourne
- DSE (Department of Sustainability and Environment) (2003) Advisory list of threatened vertebrate fauna in Victoria -2003. Department of Sustainability and Environment, Victoria
- DSE (Department of Sustainability and Environment) (2007a) Atlas of Victorian Wildlife, Department of Sustainability and Environment, Victoria
- DSE (Department of Sustainability and Environment) (2007b) Department of Sustainability and Environment, Victoria
- Emison, W.B., Beardsell, C.M., Norman, F.I., Loyn, R.H. & Bennett, S.C. (1987) Atlas of Victorian Birds. Department of Conservation Forests & Lands and RAOU, Melbourne.
- Gelman, A., Meng, J.X., Stern, H.S., 1996. Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica* **6**, 733–807.
- Gibbons, P. (1999) Habitat-tree retention in wood production forests. PhD thesis. Australian National University, Canberra.
- Gibbons, P. and Lindermayer, D.B. (2002) 'Tree hollows and wildlife conservation in Australia.' (CSIRO Publishing: Melbourne)
- Harley, D.K.P. (2004) Patterns of nest box use by Leadbeater's Possum *Gymnobelideus leadbeateri*: applications to research and conservation. In 'The Biology of Australian Possums and Gliders'. (Eds RL Goldingay and SM Jackson) pp. 318-329. (Surrey Beatty & Sons: Sydney)

- Harper, M.J., McCarthy, M.A., van der Ree, R., and Fox, J.C. (2004). Overcoming bias in ground-based surveys of hollow-bearing trees using double-sampling. *Forest Ecology and Management* 190:91–300.
- Heinze, G., and M. Schemper. 2002. A solution to the problem of separation in logistic regression. *Statistics in Medicine* 21:2409–2419.
- Inions GB, Tanton MT, Davey SM (1989) Effect of fire on the availability of hollows in trees used by the Common Brushtail Possum, *Trichosurus vulpecula* Kerr, 1792, and the Ringtail Possum, *Pseudocheirus peregrinus* Boddaerts, 1785. *Australian Wildlife Research* 16, 449-458.
- Jacobs, M.R. (1955) Growth Habits of the Eucalypts. Forestry & Timber Bureau, Canberra.
- Kalcounis-Rüppell, M.J., Pysllakis, J.M. and Brigham, R.M. (2006) Tree roost selection by bats: an empirical synthesis using metadata-analysis. *Wildlife Society Bulletin* 33, 1123-1132.
- Kavanagh, R.P. and Stanton, M.A. (1998) Bird population recovery 22 years after intensive logging near Eden, New South Wales, *Emu* 103, 221-231.
- Kavanagh, R.P. and Wheeler, R.J. (2004) Home-range of the greater glider *Petauroides volans* in tall montane forest of southeastern New South Wales, and changes following logging. In 'The Biology of Australian Possums and Gliders'. (Eds RL Goldingay and SM Jackson) pp. 413-425. (Surrey Beatty & Sons: Sydney)
- Lada H., Thomson J.R., Mac Nally R., Horrocks G., and Taylor A (2007). Evaluating simultaneous impacts of three anthropogenic effects on a floodplain-dwelling marsupial *Antechinus flavipes*. *Biological Conservation* 134: 527-536.
- Lamb, D., Smith, A., Wilkinson, G. and Loyn, R. (1998) Managing habitat trees in Queensland forests. A report by the Habitat Tree Technical Advisory Group to the Queensland Department of Natural Resources, Forest Resources.
- Law, B.S. and Anderson, J. (2000) Roost preferences and foraging ranges of the Eastern Forest Bat *Vespadelus pumilus* under two disturbance histories in northern New South Wales, Australia. *Austral Ecology* 25, 352-367.
- Lewis, S.E. (1995) Roost fidelity of bats: a review. *Journal of Mammalogy* 76, 481-496.
- Lindenmayer, D.B., Cunningham, R.B., Nix, H.A., Tanton, M.T., Smith, A.P. (1991) Predicting the abundance of hollow-bearing trees in montane forests of southeastern Australia. *Australian Journal of Ecology* 16, 91-98.
- Loyn, R.H., Lumsden, L.F. and Ward, K. A. (2002) Vertebrate fauna of Barmah Forest, a large forest of River Red Gum *Eucalyptus camaldulensis* on the floodplain of the Murray River The Victorian Naturalist 119 (3)
- Lumsden, L. and Bennett, A.F. (2004) Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia *Biological Conservation*
- Lumsden, L.F., Bennett, A.F., Silins, J.E. (2002) Location of roosts of the Lesser Long-eared Bat *Nyctophilus geoffroyi* and Gould's Wattled Bat *Chalinolobus gouldii* in a fragmented landscape in south-eastern Australia. *Biological Conservation* 106, 237-249.
- Lunn, D. J., Best, N. and Whittaker, J. (2005). Generic reversible jump MCMC using graphical models, Technical Report EPH-2005-01, Department of Epidemiology and Public Health, Imperial College London, UK.
- Mackowski, C.M. (1984) The ontogeny of hollows in Blackbutt, *Eucalyptus pilularis* and its relevance to the management of forests for possums, gliders and timber. In 'Possums and Gliders'. (Eds AP Smith and ID Hume) pp. 517-525. (Surrey Beatty and Sons: Sydney)
- Mac Nally, R. 2006. Longer-term responses to experimental manipulation of fallen timber on forest floors of floodplain forest in south-eastern Australia. *Forest Ecology and Management* 229:155-160.
- Mac Nally, R. and Horrocks, G., (2002) Habitat change and restoration: responses of a forest-floor mammal species to manipulations of fallen timber in floodplain forests. *Animal Biodiversity and Conservation*, 25.1:41-52.
- Mac Nally, R. & Parkinson, A. (2005) Fallen timber loads on southern Murray-Darling basin floodplains: history, dynamics and the current state in Barmah-Millewa. *Proceedings of the Royal Society of Victoria*, 117, 97-110.
- Mac Nally, R., Parkinson, A., Horrocks, G., Conole L. and Tzaros, C. (2001) Relationships between terrestrial vertebrate diversity, abundance and availability of coarse woody debris on south-eastern Australian floodplains. *Biological Conservation* 99, 191-205.
- MDBC (Murray Darling Basin Commission) (2003) Preliminary Investigations Into Observed River Red Gum Decline Along the River Murray Below Euston. Technical Report 03/03. Murray-Darling Basin Commission, Canberra.
- MDBC (Murray Darling Basin Commission) (2007) The Living Murray Icon Site Condition Report, October 2007. Murray-Darling Basin Commission, Canberra.

- Menkhorst, P.W. (1995) 'Mammals of Victoria: distribution, ecology and conservation' (Oxford University Press: Melbourne).
- Menkhorst, P.W. (1984) Use of nest boxes by forest vertebrates in Gippsland: acceptance, preference and demand. *Australian Wildlife Research* 11: 255-264
- Meredith, C.W. (1984) Possums or poles? – The effects of silvicultural management on the possums of Chiltern State Park, northeast Victoria. In 'Possums and Gliders'. (Eds AP Smith and ID Hume) pp. 575-577. (Surrey Beatty and Sons: Sydney)
- Milledge, D. R. & Palmer, C. L. (1990) The Sooty Owl in Mountain Ash Forests in the Victorian Central Highlands. Report to the Department of Conservation and Environment, Melbourne.
- Newton-John, J. (1992) Arboreal Habitat in River Red Gum (*E.camaldulensis*) in the Barmah Forest. University of Melbourne 41 pp (unpublished)
- Newton, I. (1994) The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70, 265-276.
- Nilsson, S.V. (1984) The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica* 15, 167-175.
- Perry, D.H., Lenz, M. & Watson, J. A. (1985) Relationship between fire, fungal rots and termite damage in Australian forest trees. *Australian Forestry*. 48: 46-53.
- Recher, H.F. (1996) Conservation and management of eucalypt forest vertebrates. In 'Conservation of faunal diversity in forested landscapes'. (Eds RM DeGraaf and RI Miller) pp.339-388. (Chapman & Hall: London)
- Rhodes, M., Wardell-Johnson, G.W., Rhodes, M.P., Raymond, B. (2006) Applying network analysis to the conservation of habitat trees in urban landscapes: a case study from Brisbane, Australia. *Conservation Biology* 20, 861-870.
- Ross, Y. (1999) 'Hollow bearing trees in native forest permanent inventory plots in south-east Queensland. Forest ecosystem research and assessment technical papers 99-23.' Department of Natural Resources, Queensland.
- Robinson, D. (1989) Conservation status of Sooty Owl and Masked Owl Unpublished report to the Scientific Advisory Committee by the CFL Flora and Fauna Group
- Rowley, I. and Chapman, G. (1991) The breeding biology, food, social organisation, demography and conservation of the Major Mitchell or Pink Cockatoo, *Cacatua leadbeateri*, on the margin of the Western Australian wheatbelt. *Australian Journal of Zoology* 39, 211-261.
- Scotts, D. J. (1991) Old-growth forests: their ecological characteristics and value to forest-dependent vertebrate fauna of south-east Australia pages 147-159 In Conservation of Australia's Forest Fauna. (ed) Lunney, D. Royal Zoological Society of N.S.W, Mosman.
- Sedgeley, J.A. (2001) Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38, 425-438.
- Smith, A.P. and Lindemayer, D. (1988) Tree hollow requirements of leadbeater's possum and other possums and gliders in timber production ash forests of the Victorian central highlands. *Australian Wildlife Research* 15, 347-362.
- Smith, A.P., Andrews, S.P., Moore, D.M. (1994) 'Terrestrial fauna of the Casino and Grafton State Forest Management Areas – descriptions and assessment of forestry impacts Northern Region State Forests of New South Wales. Casino Management Area EIS supporting document no. 6.' Forestry Commission of New South Wales, Coffs Harbour.
- Soderquist, T.R. (1999) 'Tree hollows in the box-ironbark forest. Analyses of ecological data from the Box-Ironbark Timber Assessment in the Bendigo Forest Management Area and Pyrenees Ranges.' Forests Service Technical Reports 99-3. Department of Natural Resources and Environment, Victoria.
- Tiddeman, C.R. and Flavel, S.C. (1987) Factors affecting choice of diurnal roost site by tree-hole bats (Microchiroptera) in south-eastern Australia. *Australian Wildlife Research* 14, 459-473.
- Trill, B. (1991) Box-ironbark forests: tree hollows, wildlife and management. In 'Conservation of Australia's forest fauna'. (Ed. D Lunney) pp. 119-124. (Royal Zoological Society of New South Wales: Sydney)
- Vesk, P.A., Nolan, R., Thomson, J.R., Dorrough, J.W. and Mac Nally, R. (2008) Time lags in provision of habitat resource through revegetation *Biological Conservation* 141, 174-186.
- VEAC (Victorian Environmental Assessment Council) (2007) River Red Gum Forests Investigation. VEAC publication Melbourne

Table 1. Extent of SFRI forest stand attributes (a) relative age and (b) crown size in Barmah forest and number of CFI and 2007 plots falling within stands of each classification.

	Extent in Barmah		2006 CFI plots		2007 plots	
	hectares	% of total	number	% of total	number	% of total
(a) Relative stand age						
Senescent	146.6	0.5	0	0	0	0
Late Mature	1027.1	3.8	2	6.9	1	7.6
Mature	17776.5	65.0	17	58.6	7	54.0
Uneven	7611.4	27.8	10	34.5	3	23.0
Regrowth	802.4	2.9	0	0	2*	15.4
Total	27364.1		29		13	
(b) Crown size (m)						
<5	1817.9	6.7	2	6.9	1	7.6
5-9.9	12532.0	45.9	16	55.2	3	23.1
10-14.9	12378.6	45.3	9	31.0	0	0
15-19.9	600.8	2.2	2	6.9	9	69.2
Total	27364.1		29		13	



Table 2. Vertebrate species recorded at Barmah forest that use tree hollows. Compiled from Barrett et al. 2003 and NRE 2000 End = endangered, Vul = vulnerable, LRnt= lower risk, near threatened, DD = data deficient. L = Listed under Flora and Fauna Guarantee act 1998, A = Action statement prepared for species. Vag = vagrant, I = introduced, + indicates pers. comm. Cited in Loyn et al. 2002.

Common name	Scientific name	FFG Listed	Cons. Status	Hollow requirement	Hollow size	Atlas records	Relative abundance	Estimated nest trees used per ha*
<b>Mammals</b>								
Little Forest Bat	<i>Vespadelus vulturnus</i>			dependent		99		
Chocolate Wattle Bat	<i>Chalinolobus morio</i>			use		91		
Lesser Long-eared Bat	<i>Nyctophilus geoffroyi</i>			use		71		
White-striped Freetail Bat	<i>Tadarida australis</i>			dependent		49		
Gould's Wattle Bat	<i>Chalinolobus gouldii</i>			use		47		
Southern Freetail Bat	<i>Mormopterus sp.</i>			use		37		
Common brushtail possum	<i>Trichosurus vulpecula</i>			dependent		32		0.2-11
Gould's Long-eared Bat	<i>Nyctophilus gouldi</i>			use		27		
Large Forest Bat	<i>Vespadelus darlingtoni</i>			dependent		25		
Yellow footed Antechinus	<i>Antechinus flavipes</i>			use		20	2.4 ha, Lada	
Inland Broad-nosed Bat	<i>Scotorepens balstoni</i>			dependent		18		
Common ringtail possum	<i>Pseudocheirus peregrinus</i>			dependent		10		0.4-71
Southern Forest Bat	<i>Vespadelus regulus</i>			dependent		6		
Squirrel Glider	<i>Petaurus norfolcensis</i>	L, A	End	dependent		4		
Sugar Glider	<i>Petaurus breviceps</i>			dependent		4		1-10
Eastern Freetail Bat	<i>Mormopterus sp.</i>			use		4		
Brush-tailed Phascogale	<i>Phascogale tapoatafa</i>	L, A	Vul	dependent		3		
Large-footed Myotis	<i>Myotis macropus</i>		LR	use		2		
Feathertail Glider	<i>Acrobates pygmaeus</i>			dependent		+		
<b>Reptiles</b>								
Common name	Scientific name	FFG Listed	Cons. Status	Hollow requirement	Hollow size	Atlas records	Relative abundance	Estimated nest trees used per ha*

Projected hollow availability at Barmah

Tree Goanna	<i>Varanus varius</i>		Vul	dependent	16			
Eastern Bearded Dragon	<i>Pogona barbata</i>		DD	use	7			
Carpet Python	<i>Morelia spilota metcalfei</i>	L	End	dependent	3			
<b>Birds</b>								
Brown Treecreeper	<i>Climacteris picumnus</i>		LR	dependent	362	Mac Nally	Loyn et al.	40+ *
Striated Pardalote	<i>Pardalotus striatus</i>			dependent	347			
Sulphur-Crested Cockatoo	<i>Cacatua galerita</i>			dependent	336			
Galah	<i>Cacatua roseicapilla</i>			dependent	332			
Crimson Rosella	<i>Platycerus elegans</i>			dependent	301			
White-throated Teecreeper	<i>Cormobates leucophaeus</i>			dependent	299			
Red-rumped Parrot	<i>Psephotus haematonotus</i>			dependent	196			
Superb Parrot	<i>Polytelis swainsonii</i>	L, A	End (V Aus)	dependent	195			
Sacred Kingfisher	<i>Todirhamphus sanctus</i>			use	190			
Laughing Kookaburra	<i>Dacelo novaeguineae</i>			dependent	183			
Pacific Black Duck	<i>Anas superciliosa</i>			use	71			
Eastern Rosella	<i>Platycerus eximius</i>			dependent	70			
Australian Wood Duck	<i>Chenonetta jubata</i>			dependent	70			
Grey Teal	<i>Anas gracilis</i>			use	59			
Tree Martin	<i>Hirundo nigricans</i>			dependent	47			
Long-billed Corella	<i>Cacatua tenuirostris</i>			dependent	44			
Azure Kingfisher	<i>Alcedo azurea</i>		LR	use	24			
Southern Boobook	<i>Ninox novaeseelandiae</i>			dependent	19			
Nankeen Kestrel	<i>Falco cenchroides</i>			use	18			
Estimated nest trees used per ha*								
Common name	Scientific name	FFG Listed	Cons. Status	Hollow requirement	Hollow size	Atlas records	Relative abundance	
<b>Birds (cont.)</b>							Mac Nally	Loyn et al.
Barn Owl	<i>Tyto alba</i>			dependent		12	0	
Cockatiel	<i>Nymphicus hollandicus</i>			dependent		9	0	

Projected hollow availability at Barmah

Little Corella	<i>Cacatua sanguinea</i>			dependent	8	0	
Peregrine Falcon	<i>Falco peregrinus</i>			use	6	0	
Australian Owlet-nightjar	<i>Aegotheles cristatus</i>			dependent	4	0	
Hardhead	<i>Aythya australis</i>		Vul	use	3	0	
	<i>Malacorhynchus</i>						
	<i>membranaceus</i>			use	3	0	
Pink-eared Duck							
Barking Owl	<i>Ninox connivens</i>	L, A	End	dependent	2	0	
Budgerigar	<i>Melopsittacus undulatus</i>			dependent	2, Vag	0	
Musk Lorikeet	<i>Glossopsitta concinna</i>			dependent	2	0	
Chestnut Teal	<i>Anas castanea</i>			use	1	0	
Major Mitchell's Cockatoo	<i>Cacatua leadbeateri</i>			dependent	1, Vag	0	
Blue Bonnet	<i>Northiella hamatogaster</i>			dependent	1, Vag	0	
Red-backed Kingfisher	<i>Todiramphus pyrrhopygia</i>			dependent	+, Vag	0	
Masked Owl	<i>Tyto novaehollandiae</i>	L	End	dependent	?	0	
Common Starling	<i>Sturnus vulgaris</i>			dependent	67	0	
House Sparrow	<i>Passer domesticus</i>			use	21	0	
						All hollow nesting land birds	81.5
						All land birds	251

\* According to Cooper et al. (2000) this density is indicative of good-quality habitat, actual hollows used will be much lower.

Table 3 Posterior parameters for logistic regression relating presence of hollows in individual trees to diameter at breast height (DHB).

node	mean	sd	2.50%	median	97.50%
<i>Intercepts</i>					
$\alpha_1$	-1.01	0.22	-1.45	-1.00	-0.59
$\alpha_2$	-1.84	0.26	-2.37	-1.83	-1.36
$\alpha_3$	-3.18	0.36	-3.96	-3.16	-2.53
<i>DBH effects</i>					
$\beta_1$	3.48	0.40	2.76	3.46	4.31
$\beta_2$	3.13	0.37	2.47	3.11	3.90
$\beta_3$	1.95	0.26	1.48	1.94	2.49
<i>Standard deviations</i>					
$\sigma_1$	3.08	2.28	1.22	2.49	8.59
$\sigma_2$	4.07	3.04	1.63	3.32	11.10
$\sigma_3$	0.19	0.15	0.03	0.15	0.57
Pseudo- $R^2$	464.5	5.363	452.4	464.7	474.7
	0.59		*PPP <sub>1</sub>	0.90	
	0.58		PPP <sub>2</sub>	0.69	
	0.39		PPP <sub>3</sub>	0.16	

\* PPP is posterior predicted probability, which is a measure of model adequacy (models with  $< 0.1 < \text{PPP} < 0.9$  are regarded as adequate, Gelman et al. 1996)

Table 4 Estimated densities of hollow-bearing trees in Barmah forest. Values in brackets refer to inclusion of only those 29 sites for which there were measurements in 2006 (top row).

	Trees with small hollows (# ha <sup>-1</sup> )	Trees with medium hollows (# ha <sup>-1</sup> )	Trees with large hollows (# ha <sup>-1</sup> )	Trees with hollows (# ha <sup>-1</sup> )
CFI 2006	12.5	9.3	4.0	14.6
CFI 1995	14.6 (13.2)	11.2 (9.9)	4.9 (4.1)	16.8 (15.3)
CFI 1987	13.6 (12.5)	10.5 (9.5)	4.6 (4.0)	15.6 (14.5)
CFI 1979	13.1 (11.6)	10.2 (9.0)	4.4 (3.7)	14.9 (13.2)
CFI 1965	13.9 (12.3)	10.9 (9.8)	4.6 (4.2)	15.6 (13.8)
CFI 1961	15.0 (12.0)	11.7 (9.5)	4.9 (4.0)	16.8 (13.4)
All 2007	17.2	13.9	6.3	19.1
LOT 2007	20.9	16.4	7.6	23.1
Random 2007	15.0	14.0	5.0	17.0
Regrowth 2007	3.0	2.0	2.0	3.0
Newton John 1992				15.3 - 22
Bennett et al. 1994				15.0
Lumsden et al 2002				11.5

Table 5 Posterior parameters for Bayesian growth model relating increment in diameter at breast height (DHB) to time, mean stem density and mean water table depth.

Parameter	mean	sd	2.50%	median	97.50%
$DBH_{max}$	255.7	5.5	250.2	254.1	270.4
<i>Rate model</i>					
$\beta_0$ (intercept)	-6.85	0.21	-7.38	-6.83	-6.43
$\beta_1$ (density)	-0.54	0.13	-0.83	-0.53	-0.31
$\beta_2$ (water)	-0.23	0.11	-0.51	-0.21	-0.06
$\beta_3$ (interaction)	0.06	0.06	-0.05	0.05	0.19
Random effects					
$\sigma_1$ (among plot)	0.52	0.10	0.36	0.51	0.75
$\sigma_2$ (among tree)	0.22	0.20	0.00	0.13	0.53
$\sigma_0$ (residual)	2.39	0.43	1.87	2.31	0.03
Model deviance	7438.00	314.50	6880.00	7578.00	7816.00
PPP*	0.50				
$R^2$	0.99				

\* PPP is posterior predicted probability, which is a measure of model adequacy (models with  $0.1 < PPP < 0.9$  are regarded as adequate, Gelman et al. 1996)