Suitable nesting sites for specialized cavity dependent wildlife are rare in woodlands

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ABSTRACT

Non-excavating species that prefer rare combinations of cavity traits are limited to only a fraction of the available tree cavity resource. Understanding animal preferences and quantifying the abundance of suitable cavities is fundamental to protecting non-excavators. We aimed to identify the traits of trees and cavities selected by a vulnerable, non-excavating bird, the superb parrot *Polytelis swainsonii*. We also evaluated cavity abundance and the accuracy of ground-based survey techniques (where an observer estimated the number of cavities in the canopy with binoculars from the ground). We then climbed trees to accurately identify true cavities and to measure their internal dimensions. Ground-based counts of tree cavities were correlated with the true number of cavity entrances in trees. When trees had zero cavities, ground counts overestimated their abundance, but for cavity-bearing trees ground counts underestimated their abundance. We found that superb parrot nest trees contained more cavities than random trees. Superb parrots selected cavities that were deeper, with wider floors and entrance sizes than random cavities. Cavities with the combination of selected traits comprised only 0.5% of the standing cavity resource. Our results confirm that non-excavators can be very selective about the types of trees and cavities they use for nesting. Rarity of suitable cavities may be a factor limiting the population growth and recovery of superb parrots. Without accounting for the critical information gap between what is observed on the ground, and what is in fact present in trees, effective habitat management for non-excavators may be compromised by inaccurate assessments of cavity abundance and conservation status.

1. Introduction

Tree cavities are a vital habitat resource for many threatened animal species. Animals can exhibit strong preferences for cavities with particular traits, for example, entrances small enough to exclude predators, or floor diameters that can accommodate a large brood (Goldingay, 2009; Cockle et al., 2011a; Stojanovic et al., 2017). For non-excavating species that prefer rare combinations of cavity traits, only a fraction of the available tree cavity resource is suitable (Gibbons et al., 2002), and this can in turn limit their populations (Ranius, 2000; Cornelius et al., 2008). This is because where primary cavity excavators (e. g. woodpeckers) are absent, non-excavators rely on mechanical damage and fungal decay to create cavities, but the odds of this process producing a suitable cavity are low (Cockle et al., 2011b). Mature trees

support more cavities than young ones, so older, less disturbed forests and woodlands have more cavities, higher cavity diversity, and correspondingly diverse communities of cavity-dependent animals (Lindenmayer et al., 2006). Unfortunately, global deforestation and cumulative land use change threatens persistence of mature forests and woodlands (Hansen et al., 2013) and it severely impacts cavity-bearing trees and their dependent fauna (Lindenmayer and Sato, 2018). Managing cavity abundance in deforested landscapes is a global conservation challenge because cavity availability limits population sizes of non-excavators (Newton, 1994; Cornelius et al., 2008). Understanding animal preferences and accurately quantifying the abundance of suitable cavities is fundamental to protecting non-excavators (Cockle et al., 2010, 2015), especially where deforestation of mature trees is ongoing (Politi et al., 2010). Unfortunately, this critical information is unavailable for many

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threatened cavity-dependent animals.

A major reason why this knowledge gap exists is that it can be difficult to quantify animal preferences and the abundance of suitable cavities without directly measuring them. Climbing trees to directly measure the dimensions of cavities can yield rich information about the ecology of forests (Cockle et al., 2015). Climbing trees is not always undertaken due to the effort, expense and risk involved. Consequently, knowledge of the standing tree cavity resource is sometimes mostly derived from indirect, ground-based surveys in some forests (Gibbons et al., 2002; Koch, 2008). However, ground counts can both over- and under-estimate the availability of tree cavities, and yield little or no information about the most important cavity traits for wildlife – their internal dimensions (Harper et al., 2004; Rayner et al., 2011; Stojanovic et al., 2012). The gap in knowledge between what is observable from the ground and the true availability of suitable cavities is a significant conservation problem. For example, population viability models that use inaccurate estimates of cavity abundance may set carrying capacity too high or low, skewing estimates of extinction risk. Given the importance of parameter uncertainty on population viability analysis (Brook et al., 1997), reducing inherent error in carrying capacity estimates is important. Furthermore, poor conservation outcomes are a likely result of ground counts if land managers decide which trees are felled or retained based on flawed estimates.

We address the knowledge gap between ground and climbing counts for a non-excavating cavity dependent bird. Superb parrots *Polytelis swainsonii* are vulnerable (Threatened Species Scientific Committee, 2016), and one of the main threats to the species is deforestation (Manning and Lindenmayer, 2009; Manning et al., 2013) and competition for nesting cavities (Threatened Species Scientific Committee, 2016). The superb parrot is listed as vulnerable in Australia, partly due to concerns about scarcity of suitable nest cavities (Threatened Species Scientific Committee, 2016). However, weak evidence of nest site limitation was used as to justify the species' IUCN status of 'least concern' (Birdlife International, 2020). Given that cavity abundance is a critical aspect of population limitation in birds (Newton, 1994), the availability of nesting sites is an important area of uncertainty that must be resolved to increase confidence in conservation categorizations of this species, and is a common challenge for threatened species more generally. The existing information about the availability of suitable cavities for superb parrots is conflicting. For example, based on surveys from a moving vehicle, Davey and Purchase (2004) estimated that potential nesting trees may be abundant, but this is the opposite conclusion of other work on the species (Manning et al., 2004, 2013). Furthermore, it is undocumented what internal traits of tree cavities, if any, are selected by superb parrots for nesting (Higgins, 1999). Consequently, existing estimates of carrying capacity are too weak to inform evaluation of the conservation status of superb parrots. This uncertainty has flow-on effects for on-ground management if, for example, a less threatened species is less likely to receive protection of its habitat. We aim to address this uncertainty by climbing trees to answer five questions about superb parrots and their habitat: (1) Is there a difference in the number of cavity entrances detected using ground and climbing counts? (2) What characteristics of trees predict whether they are selected by superb parrots for nesting? (3) Is there a difference between nest and random tree cavities? (4) Is there a difference in the traits of cavities between tree species? (5) What proportion of random cavities fit the criteria of a superb parrot nest?

2. Methods

2.1. Study species and area

The superb parrot is a medium-sized (~140 g) sexually dimorphic Australian bird that occurs primarily from the Riverina area in the north of the state of Victoria and the central part of the state of New South Wales and the Australian Capital Territory, to northern central New South Wales in winter (Higgins, 1999). Superb parrots nest in mature trees and there is evidence that suitable nest cavities are reused between breeding seasons (Manning et al., 2004). The species is social and, if enough breeding habitat is locally available, they nest in groups (Higgins, 1999).

Our study area was the northern part of the Australian Capital Territory where the species shows strong reliance on the endangered Yellow Box – Blakely's Red Gum grassy woodland ecological community. Our sites were located across three areas (details withheld) of grassy, open woodlands of mixed tenure, near the Canberra urban area. All sites have ongoing grazing and browsing pressure (from native wildlife and stock), so the canopy cover is predominantly mature trees with limited recruitment.

2.2. Nest identification and data collection

We identified superb parrot nests using behavioral cues of birds in potential nesting habitat (Manning et al., 2004). For every superb parrot nest identified, we identified an additional randomly selected tree that superb parrots did not use for nesting. Random trees were selected within the same area as nest trees, but we used a DBH minimum of 50 cm as a criterion for tree selection (because our field studies showed that superb parrots do not nest in trees with DBH < 50 cm). Random trees comprised at least eight individuals of each of three species used as nests by superb parrots in our study area: Blakely's red gum *Eucalyptus blakelyi*, inland scribbly gum *E. rossii* and yellow box *E. melliodora*. For both nest and random trees, we recorded both tree- and cavity-level data. At the tree-level, we recorded: (i) superb parrot nest tree yes/no, (ii) diameter at breast height (DBH) in centimeters, (iii) health as an ordinal category where 1 = perfectly healthy, 2 = early crown senescence, 3 = moderate crown senescence, 4 = severe senescence, and 5 = dead, (iv) species, (v) a ground count of the number of cavity entrances, and (vi) the true number of cavity entrances counted by climbing. We used a single ground observer to eliminate observer bias in counts. The ground observer was blind to the outcomes of climbing counts and tallied all visible cavities with a maximum estimated entrance diameter > 5 cm, estimated by eye. We used this size limit because this represented the smallest possible cavity that might interest a parrot, and be counted as potential nesting habitat by a surveyor. The ground observer used binoculars and counted cavities in each tree for as long as needed to reach a confident assessment that observed tree holes were likely to be true cavities. By definition, ground observations did not involve any attempt the measure the internal dimensions of cavities because these are not visible from the ground.

We then used single rope techniques to climb trees to count and measure all cavities accessible to a skilled climber. To count as a cavity the depth of the hole had to exceed the minimum diameter of the entrance (Stojanovic et al., 2012). We did not attempt to check all small dead branch stubs (anything smaller than a thumb diameter), and so underestimate the abundance of very small cavities. For accessible cavities, we followed Stojanovic et al. (2012) and recorded; (i) superb parrot nest (yes/no), (ii) the number of entrances, (iii) minimum diameter of each entrance hole, (iv) the distance from the bottom of each entrance to the bottom of the cavity, hereafter called depth, (v) the minimum diameter of the cavity floor, (vi) the internal diameter of the cavity 10 cm below the entrance, and (vii) the diameter of the stem containing the cavity. We tallied the true number of medium sized cavity entrances to match the ground count of potential superb parrot sized entrances.

We report sample sizes in Table 1.

2.3. Analytical approach

All analyses were conducted in R (R Development Core Team, 2020) and we used the packages emmeans (Lenth, 2018), ggplot2 (Wickham, 2016) and car (Fox and Weisberg, 2019). We selected among competing

Table 1

Summary of sampled trees (≥50 cm DBH and received both ground and climbed cavities survey) and cavities. * *E. melliodora* nest tree excluded from analysis due to low sample size. ** Includes all sampled nest trees plus additional superb parrot nests measured opportunistically.

Attribute	*E. blakelyi*	*E. melliodora*	*E. rossii*	Total
nest trees	19	1*	6	25
random trees	26	16	8	50
hollow-bearing trees	44	14	14	72
trees < 110 cm DBH	28	6	7	41
trees > 110 cm DBH	17	10	7	34
nest cavities	37	1	13	52**
random cavities	200	28	90	435

models using ΔAIC < 2 (Burnham and Anderson, 2002). We provide R markdown script in Supplementary Materials and this includes summary information about the data, and additional analytical details including AIC values and summary outputs for all models.

2.3.1. Question 1: is there a difference in the number of cavity entrances detected using ground and climbing counts?

We used the data on the total counts of cavity entrances in each tree (including only cavities with entrance diameters > 5 cm to make ground and climbing counts comparable). We used the ground counts as the response variable in generalized linear models (GLMs) with Poisson error distributions. We fitted the climbing counts and tree DBH (included as a factor: < 110 cm, hereafter small; > 110 cm, hereafter large) as main fixed effects, plus additive and interactive models of these two variables.

2.3.2. Question 2: what characteristics of trees predict whether they are selected by superb parrots for nesting?

To answer this question, we used tree-level data for both nest and random trees. We only found one superb parrot nest in a yellow box, so we excluded this species from this analysis. We used MANOVA to compare species, DBH, health, climbing count of entrances in nest and random trees in a multivariate framework. Based on the results of the MANOVA, we selected significant variables to use as fixed effects in GLMs to estimate effect sizes of the individual variables on the odds of a tree being selected for nesting by superb parrots. We used nest status of trees (yes/no) as the response variable and used a binomial error distribution for models. We fitted the climbing count of entrances, tree DBH (included again as a two-level factor) as main fixed effects, plus additive and interactive models with these variables.

2.3.3. Question 3: is there a difference between nest and random tree cavities?

We used cavity-level data to answer this question and excluded any cavities with missing data for any variable (some internal dimensions were not possible to measure for every cavity). Cavities can have more than one entrance, so we only included values for either the minimum depth (i.e. the shortest distance between a predator and the cavity floor), or in the case of superb parrot nests, the depth from their selected entrance to the floor. We used the smallest value of either the minimum entrance diameter or the internal diameter of the cavity at 10 cm distance from the bottom of the entrance, hereafter called 'entrance size'. Entrance size is important in passive nest defense (Stojanovic et al., 2017), and we summarized the data this way to account for cavities with large entrances but narrower chambers. We used MANOVA to compare the depth, entrance size, floor diameter and diameter of the stem containing nest and random cavities in a multivariate framework.

2.3.4. Question 4: is there a difference in the traits of cavities between tree species?

To address this question, we used all available cavity-level data except for records with missing data. We used MANOVA to compare the

depth, entrance size, floor diameter and diameter of the stems containing cavities between Blakely's red gum, inland scribbly gum and yellow box in a multivariate framework. We also fitted a generalized linear model with a Poisson error distribution to evaluate if the number of entrances per tree cavity varied between tree species (we considered this trait separately to estimate on a count, rather than a centimeter, scale).

2.3.5. Question 5: What proportion of random cavities fit the criteria of a superb parrot nest?

We answered this question using the cavity-level data on the subset with no missing values. We filtered out cavities that were larger or smaller than the confidence limits of the depth, entrance size, and floor diameter of superb parrot nest cavities, and calculated the proportion of random cavities (out of those measured) that were potentially suitable as nests. We derived the confidence intervals for each trait of superb parrot nest cavities from the results of Question 4.

3. Results

3.1. 1 Question 1: Is there a difference in the number of cavity entrances detected using ground and climbing counts?

Based on ΔAIC of 3.37 the best supported model contained an interaction between the climbing count of cavity entrances and tree DBH on ground counts of cavity entrances (Supplementary Materials). The estimates of means and confidence intervals from this model are presented alongside the raw data in Fig. 1. Based on this model, at climbing counts of zero cavity entrances in a tree, the predicted ground count was 1.5 for small trees and 2.5 for large trees. At climbing counts of 10 entrances, the predicted ground count was 4.4 for small trees and 5.4 for large trees.

3.2. Question 2: What characteristics of trees predict whether they are selected by superb parrots for nesting?
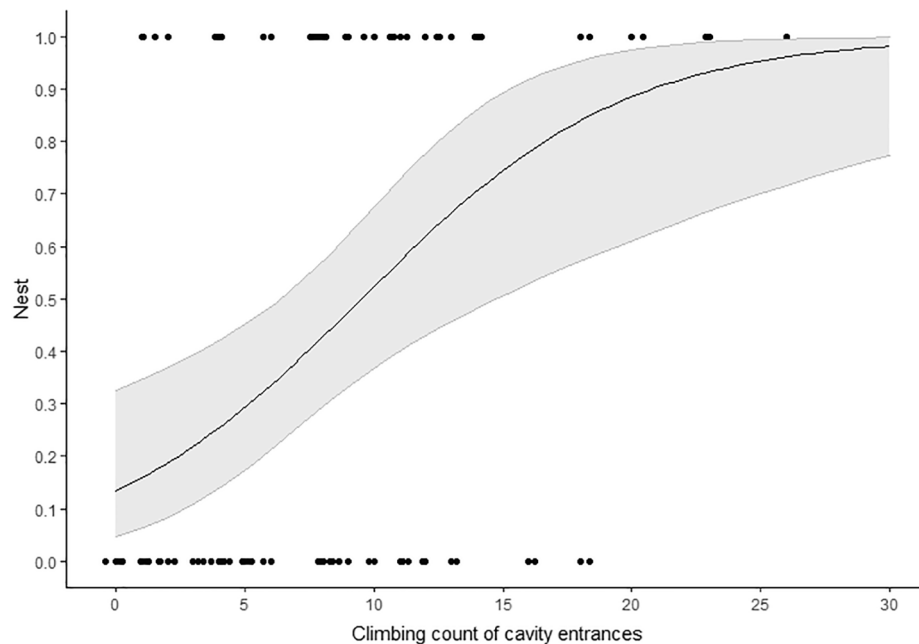
The multivariate test found significant differences in the characteristics of superb parrot nest trees and random trees (Pillai's Trace = 0.26, F = 4.79, d.f. = 4, p = 0.002). Trees differed in their DBH (d.f. = 1, F = 7.98, p = 0.006) and the climbing count of cavity entrances (d.f. = 1, F = 15.08, p = 0.0003) but not in their health or species. Of the univariate models, we found equivalent support for three models: (i) a model with only the effect of the climbing count of cavity entrances, (ii) an model with an additive effect of the climbing count of cavity entrances and tree DBH, and (iii) an interaction between the climbing count of cavity entrances and DBH (Supplementary Materials). In all models, there was a positive relationship between the climbing count of cavity entrances and the likelihood of superb parrot nesting. Both models that included tree DBH showed a positive relationship between DBH and the likelihood of nesting (effect sizes for the additive and interactive models are shown in supplementary materials). We preferred the simplest one containing only the main effect of the climbing count of cavity entrances on the likelihood that a tree had a superb parrot nest. This was our preferred model because (i) the number of cavity entrances counted from the ground was correlated with DBH (Pearson's product-moment correlation: t = 3.8, d.f. = 57, p = 0.0003), and (ii) the simplest model had the lowest AIC. Based on this model, the likelihood of a tree being used by superb parrots increased with the number of cavity entrances detected by climbing (Fig. 2).

3.3. Question 3: Is there a difference between nest and random tree cavities?

The multivariate test found significant differences in the characteristics of superb parrot nests and random cavities (Pillai's Trace = 0.05, F = 4.89, d.f. = 4, p = 0.0007). Nest and random cavities differed in their
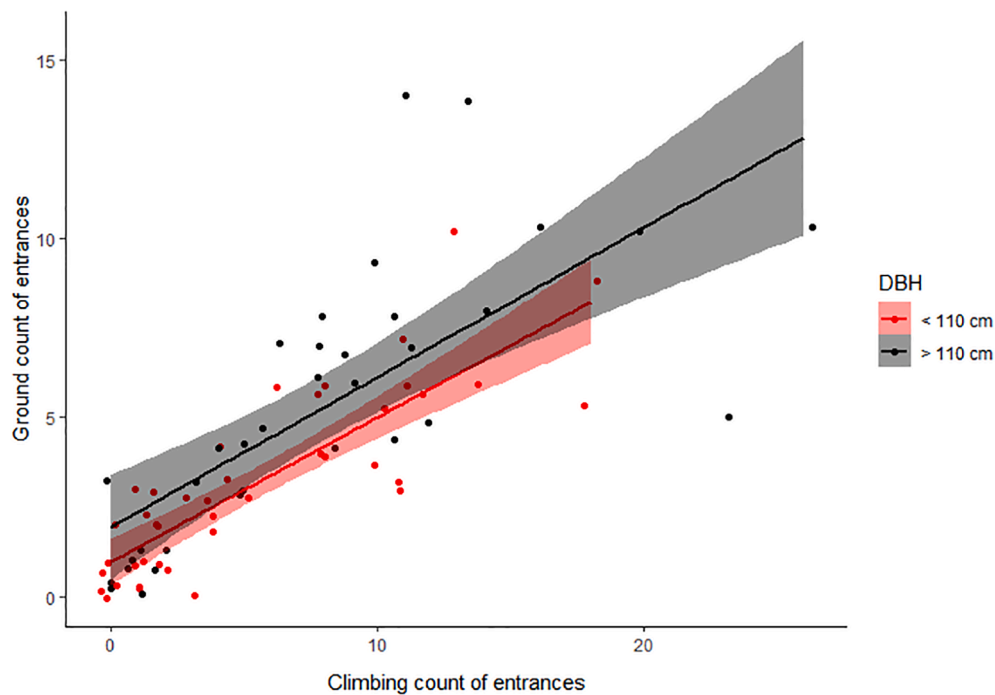
Fig. 1. Estimated means and confidence intervals for the best model of the interaction between climbing counts of entrances and tree size on the predicted number of cavity entrances counted from the ground.

Fig. 2. Modeled estimates and confidence intervals for the likelihood that a tree is a superb parrot nest tree based on the count of cavity entrances from climbing.

depth (d.f. = 1, F = 6.06, p = 0.01), floor diameter (d.f. = 1, F = 11.40, p = 0.001), and entrance size (d.f. = 1, F = 7.90, p = 0.005), and their stem diameter (d.f. = 1, F = 8.28, p = 0.004). Estimated means and confidence intervals presented in Fig. 3.

3.4. Question 4: Is there a difference in the traits of cavities between tree species?

The multivariate test found significant differences in the characteristics of cavities between tree species (Pillai's Trace = 0.08, F = 3.93, d.

f. = 8, p = 0.0001). This was largely attributable to differences in the stem diameter of cavities (d.f. = 1, F = 10.65, p < 0.0001), but depth, floor diameter and entrance size of cavities were not different between tree species (Fig. 4). There was no difference in the number of entrances per cavity between the tree species based on ΔAIC of < 2 between the null model and the one containing the effect of tree species.
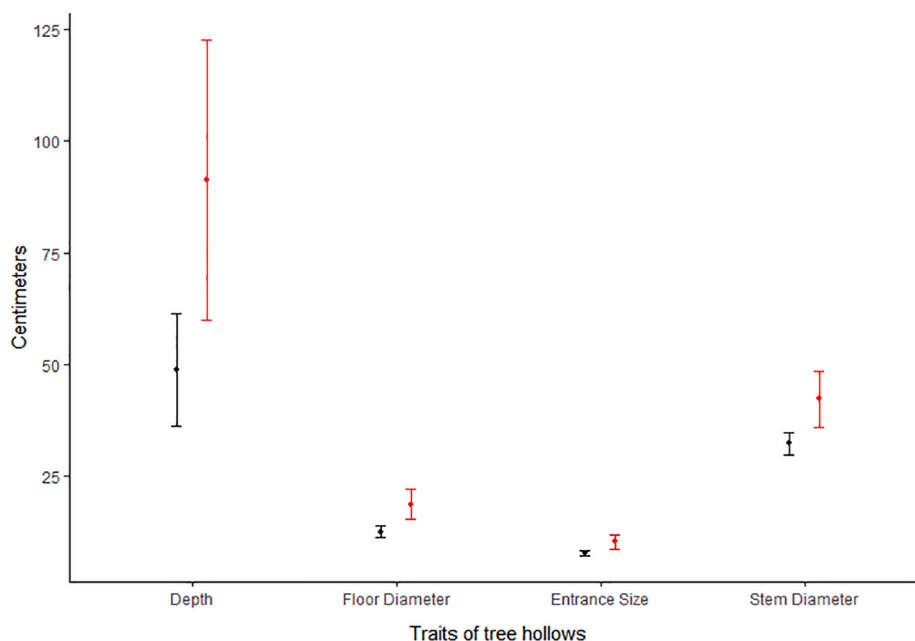
Fig. 3. Estimated means and confidence intervals for the traits of tree cavities used by superb parrots for nesting (red) and random cavities (black).
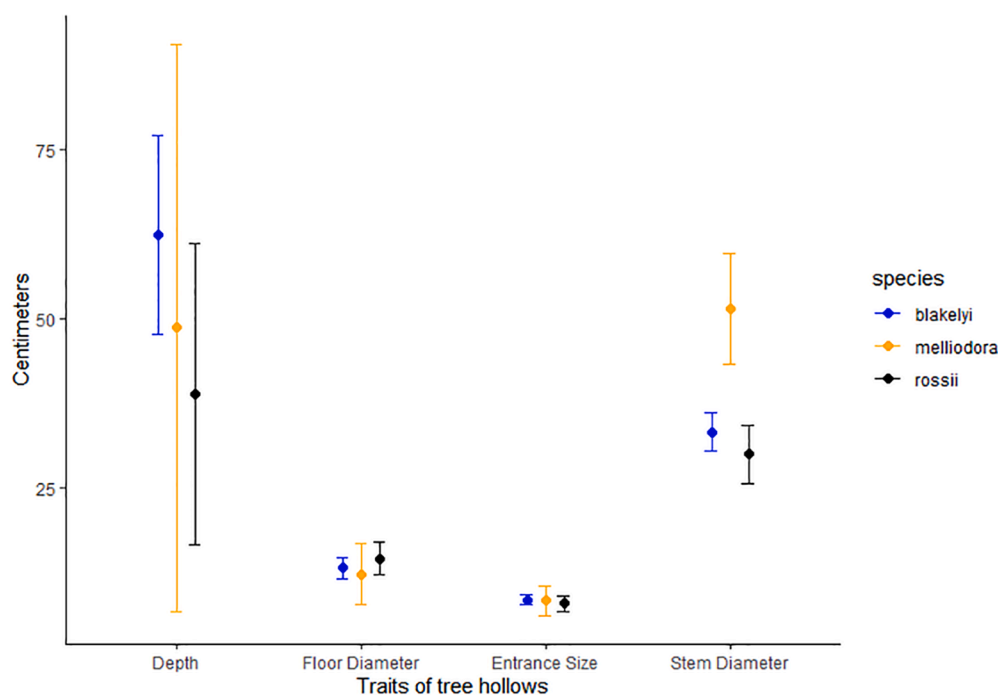

Fig. 4. Estimated means and confidence intervals for the traits of tree cavities measured between the three tree species in our study area.

3.5. Question 5: What proportion of random cavities fit the criteria of a superb parrot nest?

We used the upper and lower confidence limits for each trait of superb parrot nests (Question 3) to filter random cavities, and these were: (i) 122–59 cm for cavity depth, (ii) 22–15 cm for floor diameter, (iii) 12–8 cm for entrance size and (iv) 49–36 cm for stem diameter. For cavities with no missing data, 62 had suitable depths, 54 had suitable floors, 85 had suitable entrance sizes and 74 had suitable stem diameters for superb parrots. However, only 2 of 369 random cavities (0.5%) met all the requirements. Of these random but suitable cavities, one occurred in a tree where superb parrots had nested in another cavity. Thus, only

2% (1/50) of randomly selected trees had one cavity suitable for superb parrots.

4. Discussion

Our results reveal that superb parrots are highly selective in their choice of cavities that they use for nesting. Superb parrots selected trees with the most abundant cavities, and their nests were deeper, with wider floors, wider entrance sizes and in larger stems than random cavities. This particular combination of traits was extremely uncommon in the study area. Our results confirm those of other studies that show parrots strongly select for the traits of cavities (Stojanovic et al., 2012, 2017; de

la Parra-Martínez et al., 2015), and adds to the evidence that suitable cavities for wildlife are rare in degraded landscapes (Cockle et al., 2010, 2011b). Suitable nesting cavities in our study system are already effectively saturated, and are predicted to become more uncommon in the future (Manning et al., 2004, 2013). Worryingly, our results suggest that superb parrots may already face shortages of suitable nesting cavities (and the trees that support them), and predicted effects of habitat degradation and low tree recruitment (Manning and Lindenmayer, 2009; Manning et al., 2013) are likely to exacerbate this problem. Furthermore, even conservative past estimates of the abundance of suitable nesting sites (which were based only on ground surveys) are likely to have over-estimated the abundance of this resource (Manning et al., 2004, 2013), which has worrying implications for the species long-term survival.

The scarcity of suitable cavities for superb parrots contrasted with the over-all abundance of cavities in the landscape – only three trees in our sample had zero cavities. In line with the results of other studies (Harper et al., 2004; Rayner et al., 2011; Stojanovic et al., 2012), we found ground counts of cavity entrances were positively correlated with counts from climbing, but the accuracy of this method was low and declined as individual trees increased in hollow abundance and diversity. For the few trees that had no cavities, ground counts over-estimated the abundance of entrances, and for cavity-bearing trees, ground counts consistently underestimated the true number. Our ground observer was highly experienced in bird surveys and locating nesting hollows, and it is possible that they were conservative. Even so, the low accuracy of ground counts (and our observation that many cavities had multiple entrances) highlights the risk of superficial estimates of cavity abundance in this landscape.

So how can conservation managers evaluate the suitability of a tree for nesting superb parrots? Rather than relying on ground counts to estimate absolute numbers of tree cavities, we suggest they are used as an index, and only in combination with other tree-level traits. Other studies show that tree DBH is a good proxy for cavity abundance and suitability for non-excavators (Lindenmayer et al., 2000), but this measure was not a strong predictor of cavity abundance in our study. This is because we made an a priori assumption about nest tree suitability that skewed our sample to large, mature trees. Even though DBH was not a good predictor of cavity counts, larger trees tended to have more cavities (Fig. 1) and were more likely to support a superb parrot nest. We suggest that a precautionary approach to conservation management of superb parrot nesting habitat should focus on protecting cavity-bearing trees (where at least one cavity is detected from the ground) with DBH > 77 cm (i.e. two standard deviations below the mean nest tree DBH). Enhanced conservation outcomes may also be gained from protecting trees with 10 or more potential cavities as these trees are more likely to be a nesting site than not (i.e. probability > 0.5, Fig. 2). Tree species did not predict use of cavities by superb parrots (yellow box excluded), and the three tree species we sampled formed similar shaped cavities. Based on these results, our suggested guidelines for detecting superb parrot nests are applicable regardless of tree species (at least in the study area). Further research is needed to confirm that the selected characteristics of superb parrot nest cavities are consistent across their geographic range, and whether other superb parrot nest tree species (e. g. River red gum *E. camaldulensis*) form suitable cavities at the low rates observed in this study.

We add to the evidence that cavities suitable for non-excavators can be extremely rare. Only 0.5% of random cavities satisfied the requirements of superb parrots and only 2% of random trees had a suitable cavity. Given that superb parrots share their habitat with other non-excavators of similar body size, it is likely that competition for suitable cavities is intense. This will likely be further exacerbated by climate change, which may result in a contraction of species' range by 2050 (Manning et al., in preparation), which may exacerbate competition for nests in smaller areas of climatically suitable habitat. Nesting cavity rarity (exacerbated by competition) likely limits carrying capacity of

breeding habitat and ultimately population growth of this species. Our study raises several new questions about resource limitation in superb parrots: (i) to what extent does nest competition reduce access to rare nesting sites? (ii) is population size predicted by local carrying capacity (the number of suitable nests)? (iii) what fraction of a local population is able to breed when nesting sites are limited? (iv) if suitable cavities are unavailable, do breeders forego nesting or attempt to nest in suboptimal cavities? (v) what is the relationship between cavity traits and breeding success? Addressing these questions is important to understanding demographic rates of superb parrots in context of the results of this study. Uncertainty about nest site limitation is an important reason why the species is listed as 'least concern' by the IUCN (Birdlife International, 2020), and we provide new information to strengthen the case that the species is probably limited by lower than expected carrying capacities in degraded landscapes.

Managing the conservation needs of non-excavating animals requires good knowledge of the needs of individual species, and the dynamics of cavity creation and loss in landscapes (Lindenmayer et al., 2011; Edworthy et al., 2012). Given that non-excavating animals are disproportionately threatened globally (Gibbons and Lindenmayer, 2002), there is an urgent need to better understand the relationships between critical resource availability and wildlife populations (Martin et al., 2004; Aitken and Martin, 2008). Superb parrots exemplify how limitation of suitable tree cavities may play an under-appreciated role in influencing populations of otherwise common species. As with many other species though, there remain important gaps in knowledge about how the number of suitable nesting sites in an area may correlate with the number of birds occupying that site and/or producing young. Our study highlights the importance of detailed life history data for understanding ecology, and the challenges of managing natural resources when widely used survey techniques are of low reliability (Rayner et al., 2011). Superficial evaluation of habitat availability (e.g. ground counts) provide no meaningful information about the critically important internal dimensions of tree cavities. Without overcoming the information gap between what is observable on the ground and what is actually present in trees, it is likely that conservation outcomes for non-excavators will be negatively affected by inaccurate assessments of cavity availability.

5. Author Statement

DS and LR conceived the study. DS, LR, MC, CD, SH and GO collected the data. DS analysed the data and wrote the manuscript. LR, MC,CD, SH,RH, GO and AM contributed to writing the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118718.

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