Overlapping den tree selection by three declining arboreal mammal species in an Australian tropical savanna

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Tree cavities are important denning sites for many arboreal mammals. Knowledge of cavity requirements of individual species, as well as potential den overlap among species, is integral to their conservation. In Australia's tropical savannas, development of tree cavities is enhanced by high termite activity, and, conversely, reduced by frequent fires. However, it is poorly understood how the availability of tree cavities in the tropical savannas impacts tree cavity use and selection by cavity-dependent fauna. There has been a severe decline among arboreal mammal species in northern Australia over recent decades. Investigation of their cavity requirements may illuminate why these species have declined drastically in some areas but are persisting in others. Here we examined this issue in three species of arboreal mammals (*Trichosurus vulpecula*, *Mesembriomys gouldii*, *Conilurus penicillatus*) on Melville Island, northern Australia. We radiotracked individuals to their den sites to evaluate whether the species differ in their den tree and tree-cavity selection. The strongest influence on den tree selection was the presence of large cavities (> 10 cm entrance diameter), with all three species using larger cavities most frequently. *Conilurus penicillatus*, the smallest species, differed the most from the other species: it frequently was found in smaller, dead trees and its den sites were closer to the ground, including in hollow logs. The two larger species had broader den tree use, using larger live trees and dens higher up in the canopy. Dens of *C. penicillatus* are likely to be more susceptible to predation and destruction by high-intensity savanna fires. This may have contributed to this species' rapid decline, both on Melville Island and on the mainland. However, the apparent preference for larger tree cavities by all three arboreal species is concerning due to the limited availability of large trees across Australian savannas, which are subject to frequent, high-intensity fires.

Keywords: arboreal mammal, black-footed tree-rat, brush-tailed rabbit-rat, common brushtail possum, den sharing, mammal decline, telemetry, tree hollows

Tree cavities are an important resource for a variety of vertebrate species worldwide (Newton 1994; Remm and Lõhmus 2011). Large, old trees, in which cavities are found most commonly, have declined globally due to disturbance processes such as land clearing, logging, severe wildfire, and livestock grazing (Lindenmayer et al. 2012, 2014). Where tree populations are in decline, there typically is an associated decline in cavity-using species (Lindenmayer and Cunningham 1997; Marsden and Pilgrim 2003; Aitken and Martin 2008; Cockle et al. 2010).

Extensive research has shown that assemblages of cavity-using species display considerable den partitioning according to preferred cavity size (Lindenmayer et al. 1990; Aitken and Martin 2004; Suzuki et al. 2013). Species tend to choose cavities with entrance diameter close to body width (Gibbons et al. 2002; Goldingay 2011; Edworthy et al. 2018) to exclude both potential competitors and predators (Menkhorst 1984; Traill and Lill 1997). Strong cavity preferences can reflect lower predation pressures and cavity insulation for survival and successful breeding (Ruczynski and Bogdanowicz 2005;

Matthews et al. 2019). In general, cavity entrances at greater heights are preferred by arboreal mammals (Carey et al. 1997; Goldingay 2011). This has been postulated to be a predator-avoidance adaptation (Nilsson 1984); however, there are many arboreal predators that access and nest in cavities (Seryodkin et al. 2003; Belcher and Darrant 2006; Adamík and Král 2008; Carvalho et al. 2014).

Denning behaviors are linked to home range size and territory defense, as well as minimizing predation risk and foraging costs (Gibbons and Lindenmayer 2002; van der Ree et al. 2006). Consequently, cavity-using mammals exhibit den swapping and multiple den use behaviors (Lindenmayer and Meggs 1996; Crane et al. 2010; Bunnell 2013). Cavity sharing among closely related individuals (i.e., kin sharing) has been recorded commonly (Fairweather et al. 1987; Banks et al. 2011) and these behaviors are important to consider when determining the cavity densities required to support communities of arboreal mammals.

Despite extensive research on cavity selection by vertebrates worldwide, comparative studies are needed in landscapes with different biotic and abiotic drivers of cavity dynamics. Neotropical and Eurasian forests have primary cavity excavators, such as woodpeckers (Cockle et al. 2011; van der Hoek et al. 2017), that drive cavity development and hence the availability of these for cavity-dependent species, such as mammals (Bunnell 2013; Edworthy et al. 2018). In marked contrast, Australasia has no primary excavators, so cavities typically develop from long-term tree decay (Cockle et al. 2011). Cavities large enough for vertebrate fauna can take many decades to develop in southern Australian temperate forests, where the vast majority of research on the continent has been focused (Lindenmayer et al. 1997; Gibbons and Lindenmayer 2002). In areas where disturbances impacting cavity-bearing trees are rare, distinctive patterns of cavity-partitioning have developed due to long-term persistence of cavities; as a result, a high diversity of cavity-dependent species has been described (Goldingay 2011). In contrast, in Australia's tropical savannas, cavity development is driven primarily by abundant termites hollowing trees, although cavity-bearing trees are threatened by frequent disturbances, in particular fires (Woolley et al. 2018). Contemporary fire regimes are believed to be characterized by a greater frequency and intensity of fires than in earlier decades (Russell-Smith et al. 2003), and this has led to speculation of widespread loss of large cavity-bearing trees, and resultant impacts on biodiversity (Williams et al. 1999; Firth et al. 2010).

The ecology of tree cavities, including cavity requirements of vertebrates in Australia's tropical savannas, is a critical knowledge gap impeding effective biodiversity conservation. In recent decades, northern Australia has seen a dramatic decline of native mammals in the "critical weight range" (body mass 35–5,550 g—Murphy and Davies 2014), with arboreal mammals disproportionately affected (Woinarski et al. 2010, 2011; Fisher et al. 2014). Most arboreal mammals have contracted to the high-rainfall areas of their former ranges (Woinarski et al. 2014; Stobo-Wilson et al. 2019), where large trees and cavities are most abundant (Woolley et al. 2018). Accumulating

evidence suggests that predation by feral cats and habitat degradation by feral herbivores are key factors associated with these declines (Davies et al. 2017; Legge et al. 2019). However, it is likely that fire regimes and their impacts on the availability of large trees and den cavities also are a strong influence on the abundance and distribution of threatened arboreal species in northern Australia (Firth et al. 2010; Woolley et al. 2018).

In this study, we focused on three endemic arboreal mammal species that had extensive geographic ranges across northern Australia at the time of European arrival, but that have experienced declines in population size and range extent (Woinarski et al. 2011). The common brush-tail possum (*Trichosurus vulpecula*) is the largest of the three species (with a mean body mass of about 1,300 g in northern Australia) and is a relative generalist in diet and ecology (Kerle 1998). It has declined in central and northern Australia (Stobo-Wilson et al. 2019), although it remains abundant in much of southern Australia. It is not currently listed as threatened by the IUCN (2019) or under Australia's Environmental Protection and Biodiversity Conservation (EPBC) Act of 1999, but the northwestern Australian subspecies (*T. v. arnhemensis*) currently is being considered for listing as Vulnerable under the EPBC Act. The black-footed tree-rat (*Mesembriomys gouldii*) is one of Australia's largest rodents (body mass of about 900 g—Woinarski et al. 2014). It is restricted to northern Australia and currently listed as Vulnerable under the EPBC Act (Woinarski and Burbidge 2016). The smallest species (body mass of about 250 g), the brush-tailed rabbit-rat (*Conilurus penicillatus*), also is restricted to northern Australia (Firth et al. 2006a; Woinarski et al. 2014; Burbidge and Woinarski 2016; Davies et al. 2017) and listed as Vulnerable under the EPBC Act.

In this study, we test the hypothesis that these three arboreal species partition their den cavities and den tree use according to body size or other ecological characteristics. First, we hypothesize that the smallest species, *C. penicillatus*, will use the smallest cavities and that the largest species, *T. vulpecula*, will use the largest cavities. Second, we hypothesize that the cavities used by the three species will differ in terms of a range of ecological characteristics other than entrance diameter. We consider the implications of these results in terms of current threats to arboreal mammals in northern Australia and whether differential rarity among the three arboreal species is associated with den selection.

MATERIALS AND METHODS

Study area.—The study was conducted between April and October 2018, on Melville Island, the larger of the two main Tiwi Islands, which are located off the northern Australian coast (11.7°S, 130.9°E; Fig. 1). Melville Island is home to a number of threatened mammal species known to use tree cavities. Savannas dominated by eucalyptus trees (*Eucalyptus* and *Corymbia* species) cover around 75% of the island (Woinarski et al. 2003). The physiognomy of these savannas varies from open forest to woodland.
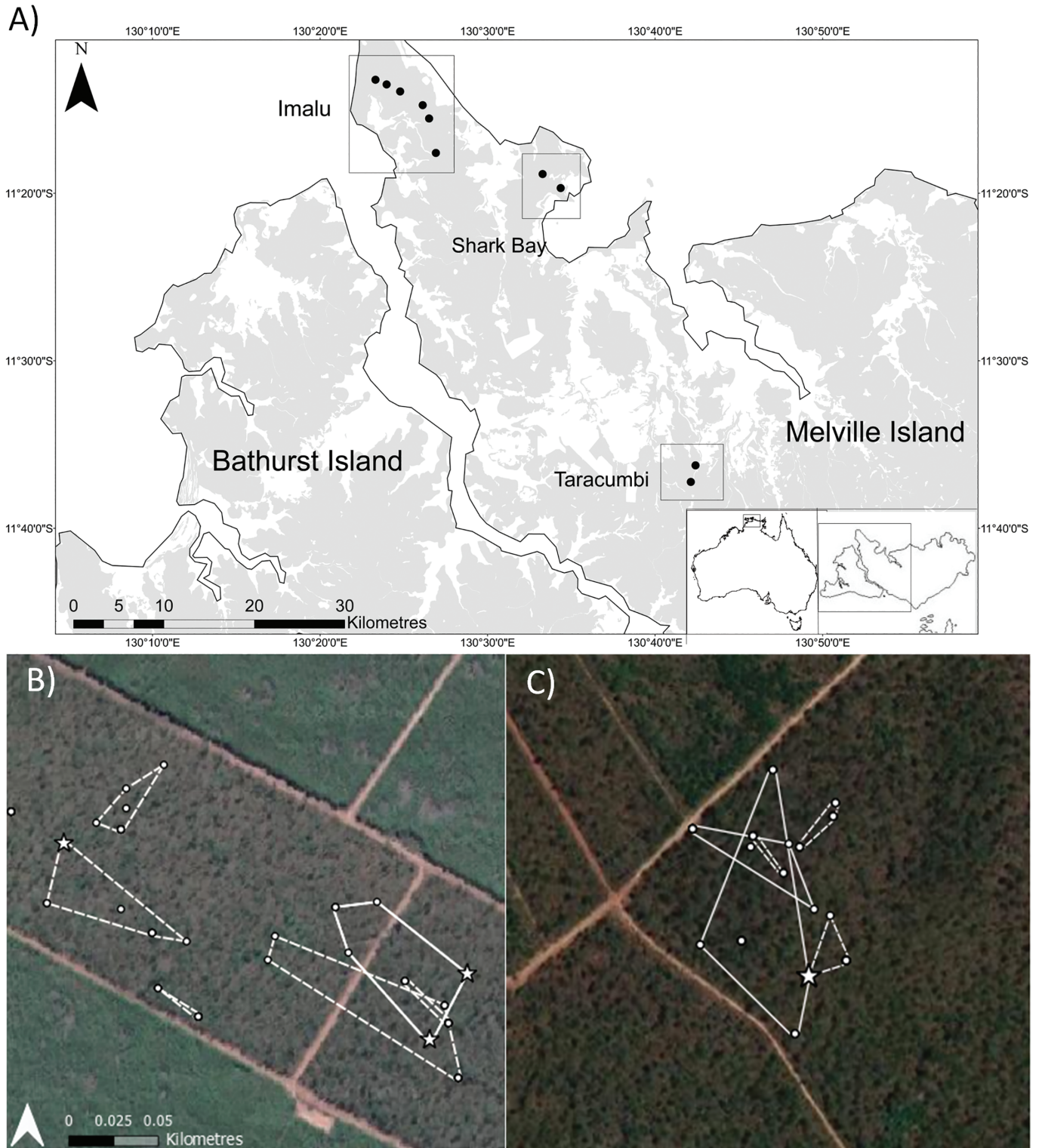
Fig. 1.—The 10 trapping locations (indicated by black dots) within our three local sites (indicated by boxes) for our radiotracking study on (A) Melville Island, off the coast of the Northern Territory, Australia. Gray shading indicates eucalypt savanna. Examples of individual minimum convex polygons of den sites at (B) Imalu and (C) Shark Bay. These two sites had multiple species radiocollared, at the Taracumbi locations there was no interspecific overlap. Line type of polygons indicate the species, with dashed line polygons representing *Conilurus penicillatus* and solid line polygons representing *Mesembriomys gouldii*. Den trees are indicated by white dots data points, and the star indicates a shared den tree used by two individuals at different times.

Three study sites were selected on the basis of knowledge from previous surveys (Davies et al. 2018; Penton et al. 2020) of the presence of tree cavities and the likely presence of arboreal mammal species. The Imalu and Shark Bay sites are located on the northwestern peninsula of the island and the Taracumbi site is situated 45 km southeast (Fig. 1). All sites were located in eucalypt savanna. Parts of the Imalu and Taracumbi study sites were burnt less than 2 months prior to the radiotracking study.

Trapping and radiotracking.—We successfully radiotracked 15 *T. vulpecula* (seven females, eight males), 13 *M. gouldii* (five females, eight males), and 15 *C. penicillatus* (seven females, eight males), totaling 43 individuals. Individuals were fitted with a VHF collar (model V1C 118C, Sirtrack Ltd., Havelock North, New Zealand), weighing 5 g. Each individual was collared only if it weighed ≥ 140 g for *C. penicillatus*, ≥ 500 g for *M. gouldii*, and ≥ 1,000 g for *T. vulpecula*, each mass being indicative of healthy adults. All three species were tracked at Imalu and Shark Bay (17 and 14 individuals, respectively). At Taracumbi, 12 individuals of *T. vulpecula* and *M. gouldii* were tracked. The 43 individuals had a minimum of one den fix to a maximum of 30 den fixes. Thirty individuals were tracked continuously for at least 2 weeks (Supplementary Data SD1). Capture and handling methods were approved by the Animal Ethics Committee of Charles Darwin University and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Sikes et al. 2016).

Dens.—We radiotracked individuals to their den locations during the day. Several individuals were "stag-watched" (cavity-bearing trees observed at dusk for emerging individuals) during May to confirm the accuracy of tracking to den trees and to identify the specific cavity from which they emerged. Location, tree species, diameter at breast height (1.3 m; DBH), tree height, and number of cavities on the tree (size classes 5–10 cm, 10–20 cm, and > 20 cm) were recorded for all dens. We used a categorical measure of tree canopy damage modified from Whitford (2002). This is a qualitative assessment of damage and health of the crown of tree, with three categories: 1 = tree alive, with little canopy damage; 2 = tree live or dead, with moderate canopy damage; 3 = tree dead, and severe canopy damage. When animals were tracked to logs on the ground, we recorded the log's diameter (at the midpoint of its length) and length, and the diameter and height of cavity entrances. When animals were tracked to the crown of the arborescent monocotyledon *Pandanus spiralis*, we recorded DBH and plant height. From the 216 dens identified, we were able to positively identify 134 cavities being used by radiotracked individuals from direct observation of the individual entering or emerging from the cavity.

Availability of den trees.—To compare den trees to the representative stand structure of the study sites, we surveyed trees at seven locations within the study sites that represented the different fire regimes that had been controlled for the previous 9 years (four locations burnt annually, two locations burnt triennially, and one location unburnt). We sampled up to 12 trees with DBH ≥ 15 cm within 50 m of the site reference point and recorded DBH, presence of cavities, and damage score.

We calculated the median DBH of the dead and live den trees for each of the species and compared this to the proportion of dead and live trees in the representative stand structure. Trees selected for comparison had to be greater than or equal to the median DBH and contain an accessible cavity.

Nearest neighbors.—To compare den trees to the closest available trees around it, we conducted nearest neighbor assessments at all 216 den locations. All assessments focused on nearest neighbor trees with DBH ≥ 10 cm within a 10-m radius around the den. Tree attributes recorded were: species, DBH, height, damage score, and the number of cavities within different size classes. Because *C. penicillatus* also used hollow logs and *M. gouldii* used *P. spiralis* as dens, these also were recorded in the 10-m radius. If two individuals had used the same den, it was recorded twice in the data set.

Data analysis.—All statistical analyses were carried out using R 3.6.2 (R Core Team, 2019). We used dens identified throughout the tracking study to investigate descriptive characteristics of dens (*n* = 226). For each den, mean DBH, tree height, total number of cavity entrances, and cavity entrance height (if identified) were calculated with standard error. We assessed reliance on cavities by comparing the frequency and percentage of cavity use by individuals that were successfully tracked for a continuous 2-week period (*C. penicillatus n* = 14, *M. gouldii n* = 10, *T. vulpecula n* = 6). We used Welch ANOVA and Games-Howell post hoc to test the hypothesis that there was a difference in the mean number of dens and mean consecutive days of using a den between the species. From these individuals, we also calculated minimum convex polygons (MCPs) of the total den area in the 2-week period using the adehabitatHRpackage in R (Calenge 2020). We recognize that MCPs usually are used for home range estimates and are affected by the length of time an animal is monitored. The data presented here represent the spatial scale of dens used by each individual only for a 2-week period to understand the number of dens required at relative scales.

We modeled the frequency of den trees (*n* = 226) relative to nearest neighbors (*n* = 1,020) using a generalized linear model (GLM) with binomial error family. Models were repeated for *C. penicillatus* dens (*n* = 74), *M. gouldii* dens (*n* = 84), and *T. vulpecula* dens (*n* = 68). Dens were used as a binary response variable (den versus neighbor). All models initially included DBH, tree height, total number of cavities, number of cavities 5–10 cm entrance diameter, number of cavities 10–20 cm entrance diameter, number of cavities > 20 cm entrance diameter, damage score, and tree species. Both of the continuous explanatory variables (DBH and tree height) were standardized by deducting the mean and dividing by twice the standard deviation (Gelman 2008). All non-eucalypts were grouped together as a single species category due to their low frequency.

Collinearity was dealt with separately for each model using an assessment of the variance inflation factors (VIFs) for each predictor. The predictor with the highest VIF was dropped and recalculated until all values were under four (Zuur et al. 2010). An information-theoretic approach to model selection was used to identify the best models according to Akaike Information

Criterion corrected for smaller sample sizes (AICc) using the MuMIn R package (Bartoń 2020). These best models were used for visualization of variable effects (ggplot2 R package—Wickham 2016; visreg R package—Breheny and Burcheet 2017). Relationships are presented for the highly influential predictors of selection by each of the three mammal species.

To determine whether there was den tree partitioning occurring between the three species, we used nonmetric multidimensional scaling (NMDS) using the R package vegan (Oksanen et al. 2019). The ordination used three dimensions and Bray–Curtis dissimilarities to model the differences among all the den trees of the three species (*C. penicillatus*, $n = 62$; *M. gouldii*, $n = 84$; *T. vulpecula*, $n = 68$). For this purpose, we removed dens in logs for *C. penicillatus*, and *P. spiralis* for *M. gouldii*. Den tree characteristics used were DBH in cm, tree height in m, and damage score.

RESULTS

Variation in dens.—We identified a total of 226 dens: 73 dens for *C. penicillatus* (15 individuals); 84 dens for *M. gouldii* (13 individuals); and 68 dens for *T. vulpecula* (15 individuals). Most dens for *C. penicillatus* were cavities in dead trees (66%). Other dens included cavities in live trees (19%) and cavities in logs (15%). *Mesembriomys gouldii* was found predominantly in cavities in live trees (54%), followed by dead trees (30%), and *P. spiralis* (17%). *Trichosurus vulpecula* mainly denned in cavities in live trees (65%), followed by dead trees (32%), and one individual twice nested in a drey (i.e., nest of dried twigs) in an exotic plantation tree (*Acacia mangium*).

Cavity size classes.—*Conilurus penicillatus* was most frequently recorded using medium–large cavities (20% of cavities 10–20 cm and 63% > 20 cm entrance diameter out of 46 cavities). *Mesembriomys gouldii* and *T. vulpecula* used only medium–large cavities (58% of cavities 10–20 cm and 42% > 20 cm entrance diameter out of 40 cavities and out of 48 cavities, respectively).

Reliance on cavities.—*Conilurus penicillatus* was found denning in dead trees 77% of the time; live trees, 14%; and hollow logs, 9%. *Mesembriomys gouldii* denned in live trees 74% of the time; dead trees, 15%; and *P. spiralis*, 11%. *Trichosurus vulpecula* denned in live trees 70% of the time; dead trees, 29%; and exposed dreys, 1%. Overall, *C. penicillatus* always was found denning in cavities either in trees or logs. *Mesembriomys gouldii* and *T. vulpecula* were found denning in tree cavities 89% and 99% of the time, respectively.

Denning area.—The total den areas comprising all daily dens over a 2-week period are presented in Supplementary Data SD1. The composite maps indicate that there was considerable overlap of total den area for individuals of all species and sexes (Figs. 1B and 1C). The dens of an individual *C. penicillatus* on average covered an area of 0.52 ha (females = 0.57 ha; males = 0.49 ha); for *M. gouldii*, 7.63 ha (females = 1.41 ha; males = 11.78 ha); and for *T. vulpecula*, 1.58 ha (females = 0.86 ha; males = 1.94 ha).
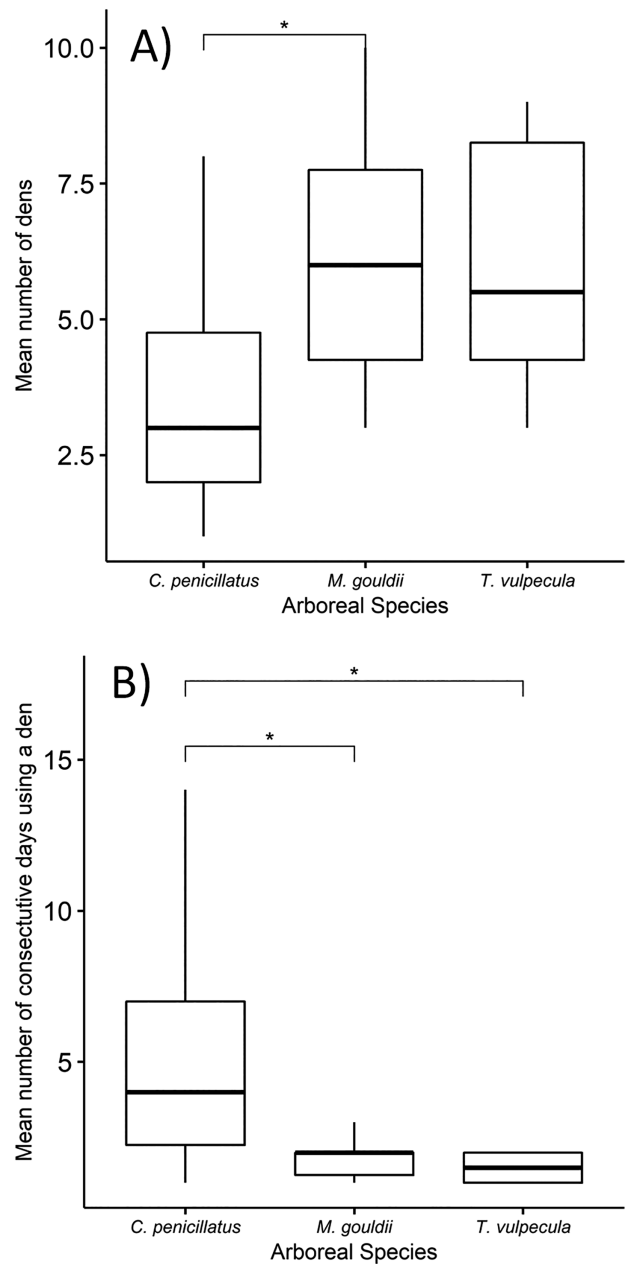

Fig. 2.—Mean number of dens (A) and number of consecutive days using a single den (B) in the 2-week radiotracking period for three species of arboreal mammal (*Conilurus penicillatus*, *Mesembriomys gouldii*, and *Trichosurus vulpecula*), on Melville Island, Australia (see Supplementary Data SD1). Box plots show the median (thick horizontal line), first and third quartiles (boxes), and range (whiskers) of measurements. Significant differences are indicated by the asterisks.

Den swapping and sharing.—There was a significant difference between the mean number of dens used among species, and the mean number of consecutive days an individual used a single den (Fig. 2A [$F_{2,12} = 5.9$, $P = 0.014$] and Fig. 2B [$F_{2,16} = 5.6$, $P = 0.016$]). Pairwise comparisons indicated significant differences between *C. penicillatus* and *M. gouldii* in the mean number of dens used ($P = 0.014$), and between *C. penicillatus* and both *T. vulpecula* ($P = 0.012$) and *M. gouldii* ($P = 0.019$) for the mean number of consecutive days an individual used a

single den (Figs. 2A and 2B). We found no significant difference between males and females within species groups. Eight den trees were used by more than one individual. Male/female pairs of *M. gouldii* and *T. vulpecula* co-occupied some dens (two pairs of *M. gouldii* and one of *T. vulpecula*); both individuals co-occupying the same tree also were recorded making reoccurring visits to the den tree separately. There were three den trees where two different individuals of *C. penicillatus* were recorded using the same den tree on separate occasions. Finally, three den trees had two different species (*C. penicillatus* and *M. gouldii*) using them on separate occasions.

Availability and characteristics of den trees.—The representative stand structure of the study sites showed that 45% of trees were cavity-bearing, but that the trees targeted by arboreal mammals for denning were among the largest 25% of live trees recorded. Dead trees represented 9% of the stand structure, and large (> 20 cm DBH) dead trees only 3% of the stand structure. Live trees were larger than dead trees on average (Fig. 3). *Conilurus penicillatus* used dead and live trees that were smaller than those used by *M. gouldii* and *T. vulpecula* (Fig. 3). Known cavity heights of *C. penicillatus* were less than 6 m from the ground on average and cavities of *M. gouldii* and *T. vulpecula* were higher on average (Table 1). Of the live den trees, *C. penicillatus* and *M. gouldii* were predominantly found denning in *Eucalyptus tetrodonta* (64% and 40%, respectively),

while *T. vulpecula* most commonly were found in *E. miniata* (48% of the time). Overall, 92% of the live trees identified as den trees in this study were eucalypts.

Predictors of den trees.—Important den tree characteristics for *C. penicillatus* included DBH, damage score (high), and number of cavities present in each size class. For *M. gouldii*, tree height and number of cavities present in each size class were important predictors of use. For *T. vulpecula*, the only important den tree characteristic was the number of cavities present in each size class (Table 2). From the best model, significant variables influencing den tree selection by *C. penicillatus* was the number of cavities present from each size class with the larger size classes more strongly influential (> 20 cm in entrance diameter). *Mesembriomys gouldii* likewise was influenced by number of cavities present, with the strongest influence being the presence of cavities 10–20 cm and > 20 cm in diameter. However, tree height also was a significant predictor. Finally, den selection by *T. vulpecula* was significantly influenced only by the number of cavities in the 10–20 cm and > 20 cm entrance diameter classes (Table 2). Overall, the number of cavities in the 10–20 cm and > 20 cm entrance diameter classes were the most highly influential explanatory variables for den tree selection by all three species, with the addition of tree height for *M. gouldii* (Fig. 4). This was similarly reflected when all species' dens were modeled against nearest neighbors (Fig. 4).

Compositional differences among den trees.—Plotting the NMDS ordination illustrated a distinction in den tree composition between arboreal species (Fig. 5). The NMDS reached a stress level of 0.03 with *C. penicillatus* being most dissimilar to *M. gouldii* and *T. vulpecula*. *Conilurus penicillatus* was associated with smaller and shorter trees than *M. gouldii* and *T. vulpecula*, with trees more likely to be higher in damage score.
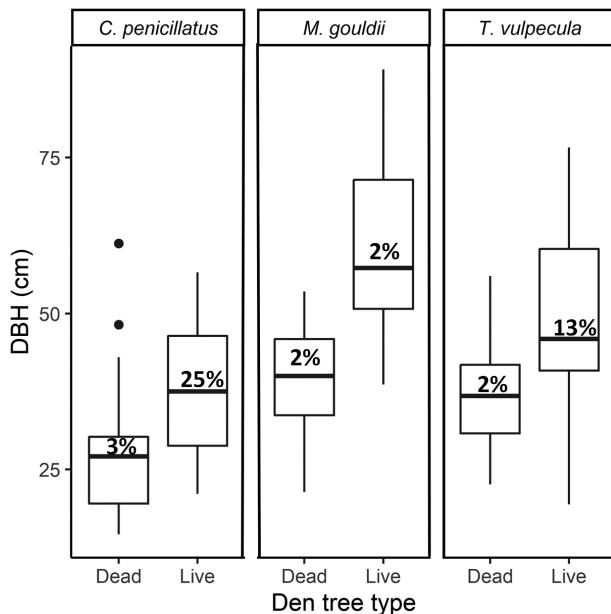
DISCUSSION

Compared to other biomes supporting assemblages of cavity-dependent mammals, we have found Australia's tropical savannas to exhibit a high degree of overlap in the sizes of cavities used by the three dominant species of arboreal mammals. All three species tended to select large cavities (entrance diameter > 10 cm), and there was little evidence of a tendency for smaller species to select smaller cavities. This is in marked contrast to patterns elsewhere in Australia, particularly in southern temperate forests, where there is a pattern of mammal body size being positively correlated with cavity entrance size, particularly for smaller species (< 1 kg body mass—Menkhorst 1984; Traill and Lill 1997; Goldingay 2011). We hypothesize that this is because large, old trees are relatively rare in Australia's tropical savannas. Such trees are capable of supporting an abundance of diverse cavity sizes and types (i.e., main stem, living and dead branches, basal, and fissures). It is well-established that high-intensity savanna fires cause high rates of mortality in both the smallest and largest trees, leading to a homogeneous stand structure strongly dominated by medium-sized trees (20–40 cm DBH—Williams et al. 1999; Lehmann et al. 2009;

Fig. 3.—Diameter at breast height (DBH) of dead and live trees identified as containing dens of three species of arboreal mammal (*Conilurus penicillatus*, *Mesembriomys gouldii*, and *Trichosurus vulpecula*), on Melville Island, Australia, during the study period (195 trees of 226 total dens). These have been separated based on arboreal species (*C. penicillatus*: *n* = 60, *M. gouldii*: *n* = 68, *T. vulpecula*: *n* = 67). Numbers above the median lines represent the percentage of trees that were randomly sampled exhibited that same characteristics as den trees (equal or greater than the median DBH and presence of cavities). Box plots show the median (thick horizontal line), first and third quartiles (boxes), range (whiskers) of measurements, and black circles are outliers.

Table 1.—Descriptive statistics of den trees ($n = 226$) identified during radiotracking of the three arboreal mammal species (*Conilurus penicillatus*, *Mesembriomys gouldii*, and *Trichosurus vulpecula*), on Melville Island, Australia. Tree characteristics include mean diameter at breast height (DBH), tree height, and total number of cavities identified from ground-based surveys of all dens ($n = 226$). Mean cavity height is based on known cavities used by radiotracked individuals ($n = 134$).

Species	Type of den tree	Tree DBH (cm ± *SE*)	Tree height (m ± *SE*)	Cavity height (m ± *SE*)
C. penicillatus	Dead trees ($n = 49$)	27.0 ± 1.3	8.7 ± 0.5	6.4 ± 0.5
	Live trees ($n = 14$)	37.0 ± 3	14.6 ± 1.2	5.9 ± 0.9
M. gouldii	Dead trees ($n = 25$)	39.7 ± 1.7	12.9 ± 0.9	10.2 ± 1.1
	Live trees ($n = 45$)	60.9 ± 1.9	19.0 ± 0.6	9.6 ± 1.1
T. vulpecula	Dead trees ($n = 22$)	36.6 ± 1.8	10.8 ± 1.0	8.1 ± 1.1
	Live trees ($n = 44$)	49.7 ± 2.2	17.5 ± 0.5	10.3 ± 0.6

Table 2.—Model selection based on Akaike Information Criterion (AICc) to test the effects of predictor variables on den selections at the tree level of three species of arboreal mammal (*Conilurus penicillatus*, *Mesembriomys gouldii*, and *Trichosurus vulpecula*), on Melville Island, Australia. The values in the table are relative variable importance values (w_+), equivalent to the sum of Akaike weights (Akaike weight is the probability that model i is the best model) for all models containing a given predictor variable. Highly influential variables have $w_+ \geq 0.73$ (equivalent to an AIC difference of 2) and are indicated in bold. N/A indicates it was not run in the model due to excessive collinearity. DBH = diameter at breast height.

Response variable	DBH (cm)	Tree height (m)	Damage score	Number of 5–10 cm cavities	Number of 10–20 cm cavities	Number of > 20 cm cavities
C. pencillatus den selection	**0.94**	0.18	0.71	**1.00**	**1.00**	**1.00**
M. gouldii den selection	0.30	**1.00**	N/A	**1.00**	**1.00**	**1.00**
T. vulpecula den selection	0.32	N/A	N/A	**0.79**	**1.00**	**1.00**

Prior et al. 2009). We hypothesize that such a stand structure leads to a low diversity of tree cavity sizes and types, which limits the ability of arboreal mammals to specialize in terms of the characteristics of the cavities that they use.

The selection of large cavities in tropical savannas also may reflect their capacity to buffer daytime temperatures. Isaac et al. (2008) found that in tropical woodlands, *T. vulpecula* select larger cavities, which tend to have a cooler and more stable microclimate than smaller cavities. The capacity of cavities to buffer maximum temperatures increases with their depth, width, and height above the ground, as well as tree diameter (Isaac et al. 2008). Indeed, we found that three of our study species selected larger cavities, and both *M. gouldii* and *T. vulpecula* used higher cavities on larger trees. This is analogous to cavity selection by arboreal vertebrates in cool, temperate climates, where large, deep cavities that retain heat in winter are favored strongly (Sedgeley 2001).

Den partitioning based on cavity entrance diameter has been suggested as a means of avoiding both competitors and predators. For example, the threat posed from predation by arboreal monitor lizards (*Varanus* spp.) has been proposed to drive a strong preference for small cavities in southeastern Australian marsupials (Soderquist 1993; Goldingay 2011). However, our smallest species, *C. penicillatus*, frequently used (63% of the time) very large cavities (> 20 cm entrance diameter). Arboreal monitors in northern Australian savannas are smaller than their southern counterparts (King and Green 1999) and may be able to access smaller cavities (< 10 cm entrance diameter). It is likely that there is comparatively less selective pressure due to predation by monitors on mammals as their diet largely consists of insects and small lizards; however, monitors are considered

flexible and opportunistic foragers (Shine 1986; Christian et al. 1996). Furthermore, the abundance of other arboreal reptiles in tropical savannas, including mammal-eating snakes, may cause additional predation pressure on arboreal mammals. Antipredator strategies for arboreal mammals therefore may favor larger cavities in tropical savannas so that predators cannot block and trap prey in cavities with smaller entrances.

There also is some evidence of den separation being driven by interspecific competition in northern Australia with the decline in cavity resources. In fragmented savannas in peri-urban areas of the City of Darwin (*ca*. 80 km south of our study site), and where cavity densities are much lower than in continuous savanna woodland, *M. gouldii* use smaller cavities than *T. vulpecula*; this has been attributed to competition between the species (Pittman 2003). Melville Island is one of the last areas of northern Australia that supports an intact arboreal mammal assemblage, and tree cavities appear to be more abundant there than in other parts of northern Australia (Woolley et al. 2018; Penton et al. 2020). We suspect that den separation, in terms of cavity entrance diameter, occurs only where tree cavities are much less abundant, leading to interspecific competition.

Despite all three species of arboreal mammals using similar-sized cavities, we did see some evidence of den separation in relation to other den tree characteristics, such as tree height and tree health (Fig. 5). The smallest of the arboreal species, *C. penicillatus*, had a strong tendency to den in dead trees (78% of all dens) and logs, relative to other species, and also was found to den at lower heights in the tree. Firth et al. (2006b) as well reported *C. penicillatus* denning in dead trees on the Tiwi Islands, not as frequently, however, as recorded in our study. In the study by Firth et al. (2006b), *C. penicillatus* frequently
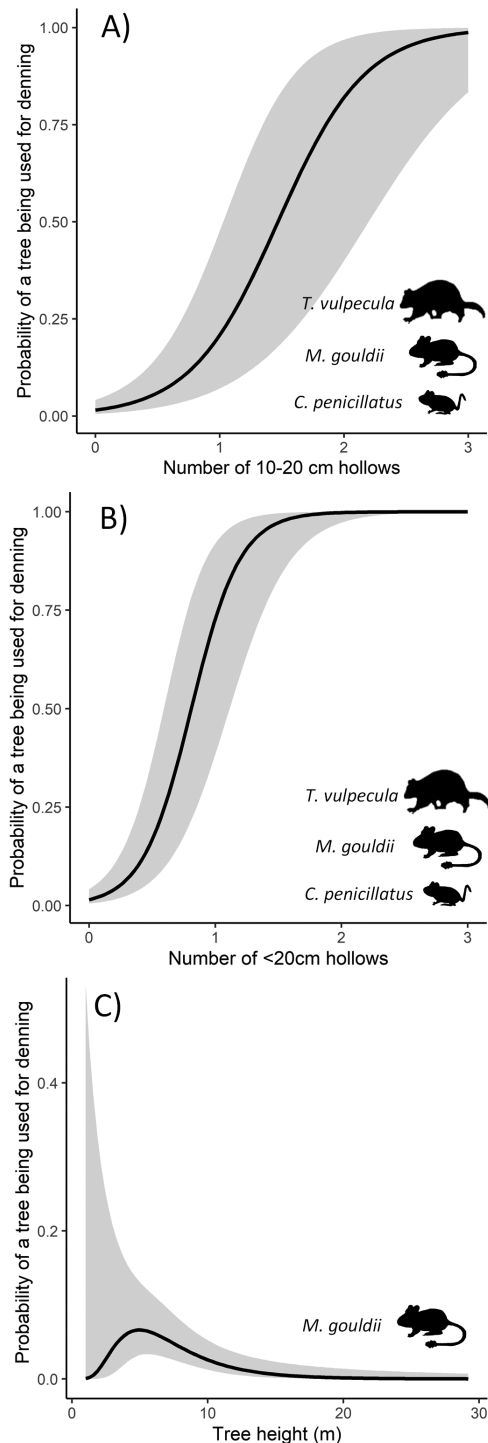
Fig. 4.—Predictions of generalized linear models of the probability of a tree being a den site for three species of arboreal mammals (*Conilurus penicillatus*, *Mesembriomys gouldii*, and *Trichosurus vulpecula*), on Melville Island, Australia, in relation to important explanatory variables: (A) the number of medium-sized cavities (10–20 cm entrance diameter) in the tree (all three species); (B) number of large cavities (> 20 cm entrance diameter) in the tree (all three species); and (C) tree height (*M. gouldii*). The black line indicates the predictions of the model and the gray band indicates the 95% confidence interval.

was found denning in live trees, prominently *E. tetrodonta*, which has thick, fibrous bark that might be preferred for ease of climbing. As there was no significant selection for particular tree species, we suspect that the use of smaller eucalypts is influenced by high termite activity accelerating cavity development in tropical savannas relative to southern Australian forests (Woolley et al. 2018). *Mesembriomys gouldii* and *T. vulpecula* were found in larger trees than *C. penicillatus* (Fig. 3), and the entrance heights of cavities they occupied were greater than those of *C. penicillatus* (Table 1). Most dead trees used by *C. penicillatus* were in the final stages of decay, with the trunks of these trees having been snapped, resulting in large cavities at lower heights. We are unable to conclude whether dead trees and logs are preferred, or whether this high rate of use merely is a reflection of interspecific displacement.

The typical den sites of *C. penicillatus* (dead trees, logs, and tree cavities, close to the ground) may make this species particularly vulnerable to declines across the region. Dead trees and logs are likely to be particularly susceptible to the frequent surface fires that characterize the high-rainfall savannas of northern Australia. Fire regimes dominated by frequent, large high-intensity wildfires are considered one of the key threatening processes for many of the threatened mammals across northern Australia (Andersen et al. 2005; Ziembicki et al. 2015), and for *C. penicillatus* in particular (Firth et al. 2010; Woinarski et al. 2014). In northern Australia, it has been demonstrated that feral cats preferentially select recently burnt areas for hunting, particularly areas of high fire severity (McGregor et al. 2016a, 2016b). *Conilurus penicillatus* on average used fewer dens and spent more consecutive days at the same den than *M. gouldii* and *T. vulpecula* (Figs. 2A and 2B). We recorded multiple individuals of *C. penicillatus* using only one den site in a 2-week period. Low densities of cavities could prevent den swapping by *C. penicillatus*, given their gregarious nature and small home range size, causing greater exposure (Laurance 1990; Firth et al. 2006b). This sedentary denning behavior could make *C. penicillatus* more susceptible to predation (including native predators such as goannas and pythons, and feral cats—Taylor et al. 2003; Isaac 2005; McComb et al. 2019). Indeed, there is recent evidence from southern Australia of feral cats targeting arboreal mammals as they emerge from their dens (McComb et al. 2019); presumably it would be easier for cats to target dens that are closer to the ground. In addition, the tendency of *C. penicillatus* to forage on the ground (for a diet predominantly of grass seeds), where it is more vulnerable to predation by cats, could partially explain its severe decline on the Australian mainland (Firth et al. 2005, 2006b; Leahy et al. 2015; McGregor et al. 2016a; Davies et al. 2017).

Although *M. gouldii* and *T. vulpecula* denned predominantly in large, live eucalypts (74% and 70% of all dens, respectively), there were differences between these two species in terms of characteristics of dens and den trees used. Den trees of *M. gouldii* were the largest recorded of the three mammal species and, as found by Griffiths et al. (2002), were predominantly *E. tetrodonta*. *Mesembriomys gouldii* was
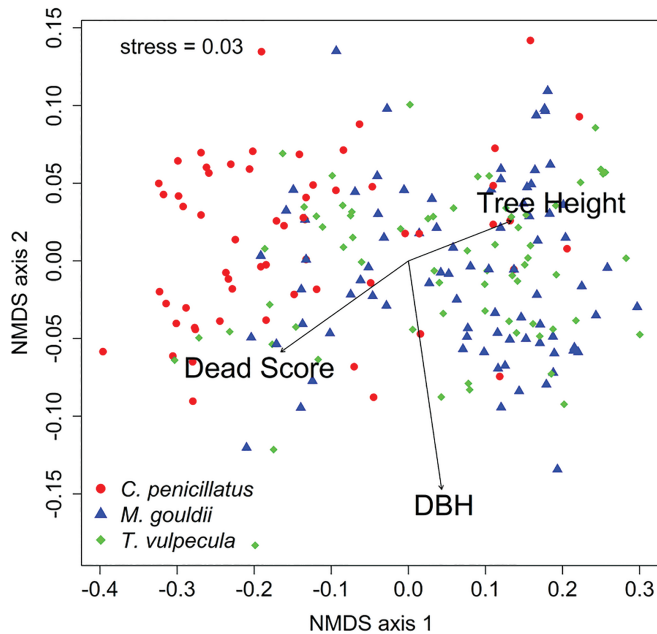
Fig. 5.—Scatterplot of the first two axes of the ordination using nonmetric multidimensional scaling (NMDS), based on den tree characteristics of three species of arboreal mammal (*Conilurus penicillatus*, *Mesembriomys gouldii*, and *Trichosurus vulpecula*), on Melville Island, Australia: diameter at breast height (DBH), tree height, and tree health. Den trees for the three arboreal species are shown separately. The black lines indicate vectors of the den tree characteristics.

found sporadically nesting in *P. spiralis* during the day and is well-known to have a regular diet of *P. spiralis* fruits (Friend 1987). In the past, *M. gouldii* were hunted by Aboriginal people, and were searched for in the dead leaves or "skirt" of *P. spiralis*, in addition to tree cavities (Friend 1987; PWCNT 1998). The den trees of *T. vulpecula* were larger than the average tree in these savannas, and, although there was no significant preference for tree species (Table 2), *E. miniata* was most commonly used. We twice recorded *T. vulpecula* using dreys; this behavior is seen commonly in the urban and periurban Darwin area, where there is low cavity availability and there are high densities of this species. Overall, the frequent use of eucalypts and dead trees likely reflects the propensity of cavity development and greater likelihood of cavity availability in these species, especially when branches are damaged, or the tree is dead and decaying (Woolley et al. 2018; Penton et al. 2020). Densities of large cavities could influence the frequency of alternative dens for *M. gouldii* and *T. vulpecula*. Areas containing lower densities of large cavities could result in a greater exposure to predation, particularly after fire.

Den sharing, both with kin and nonkin, has been recorded for many arboreal mammal species in eucalypt forests and woodlands of southern Australia (Fairweather et al. 1987; Handasyde and Martin 1996; Smith et al. 2007). Consistent with this, we found den sharing between male and female pairs of *M. gouldii* and *T. vulpecula*. Firth et al. (2006b) recorded an instance of a radiotracked female *C. penicillatus* sharing a den with another adult female. However, we did not record

any instances of multiple adults of *C. penicillatus* sharing a den. We did record interspecific synchronous den sharing (i.e., more than one species in the den at the same time) between breeding pairs of *M. gouldii* and *T. vulpecula*, which could indicate a high level of social tolerance or adequate cavity densities (Banks et al. 2011). Although there is no direct evidence of interspecific competition for tree cavities in the tropical savannas, our understanding of this aspect of the ecology of the arboreal mammal community is still very limited, and further research is required to determine the influence of competition on den use patterns.

We found three cavities that were used by individuals of different species but on different occasions (*M. gouldii* and *C. penicillatus*). Interspecific cavity use has been recorded in the Americas and Europe (Aitken et al. 2002; Bonaparte and Cockle 2017) in cavity-nesting communities with substantial den overlap, indicating co-occurring taxa can exploit the same types of cavities (Balen et al. 2002; Sarà et al. 2005; Cockle et al. 2010; Kobayashi et al. 2014). It was unclear from our study whether *M. gouldii* were aggressively outcompeting *C. penicillatus* for these cavities, or whether *C. penicillatus* were opportunistically denning if *M. gouldii* were not present. However, *M. gouldii* was found most frequently denning in these shared dens during our radiotracking period. Larger tree cavities (≥ 10 cm entrance diameter) are much less abundant in Australian savannas than small cavities (< 10 cm entrance diameter): 22 ha^{-1} versus 80 ha^{-1}, respectively, on Melville Island (Woolley et al. 2018; Penton et al. 2020). It therefore is unclear whether arboreal mammals are competing for a limited supply of large tree cavities or whether cavity height is significant enough to partition den use. High cavity overlap could increase the risk of interspecific competition, which could negatively affect arboreal populations if cavity densities were to change unfavorably in woodland savanna.

Most cavity-dependent mammal species of the tropical savannas of northern Australia have severely contracted to the high-rainfall parts of their former ranges (Woinarski et al. 2014; Stobo-Wilson et al. 2019), to areas where large trees and cavities remain most abundant (Woolley et al. 2018). There still is insufficient information to assess whether this is a causal relationship or is associated with other factors, e.g., higher availability of resources, such as food and shelter, or lower densities of feral predators. Frequent, intense fires in northern Australian savannas have been suspected of reducing cavity availability, given the ease with which intense fires can kill large, old trees (Williams et al. 1999; Liedloff and Cook 2007). The influence of fire regimes on the long-term availability of tree cavities, and whether cavity-dependant mammal species are limited by the abundance of large tree cavities, is a key unresolved question. Resolving it would help us to understand whether current modes of fire management being rolled out across northern Australia, that make use of extensive prescribed burning to reduce greenhouse gas emission from high-intensity wildfires (Russell-Smith et al. 2013), can benefit arboreal mammals by helping cavity-bearing trees to persist in flammable savanna landscapes (Corey et al. 2019).

Acknowledgments

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Area of minimum convex polygons (MCPs 100%) of den sites and number of dens used by individuals of three species of arboreal mammal (*Conilurus penicillatus*, *Mesembriomys gouldii*, and *Trichosurus vulpecula*) tracked for 14 days at three sites on Melville Island, Australia.

Literature Cited

Adamík, P., and M. Král. 2008. Nest losses of cavity nesting birds caused by dormice (Gliridae, Rodentia). Acta Theologica 53:185–192.

Aitken, K. E. H., and K. Martin. 2004. Nest cavity availability and selection in aspen-conifer groves in a grassland landscape. Canadian Journal for Forest Research 34:2099–2109.

Aitken, K. E. H., and K. Martin. 2008. Resource selection plasticity and community responses to experimental reduction of a critical resource. Ecology 89:971–980.

Aitken, K. E. H., K. L. Wiebe, and K. Martin. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. The Auk 119:391–402.

Andersen, A. N., et al. 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. Austral Ecology 30:155–167.

Balen, J. H., C. J. H. van Booy, J. A. van Franeker, and E. R. Osieck. 2002. Studies on hole-nesting birds in natural nest sites. Ardea 70:1–24.

Banks, S. C., D. B. Lindenmayer, L. McBurney, D. Blair, E. J. Knight, and M. D. Blyton. 2011. Kin selection in den sharing develops under limited availability of tree hollows for a forest marsupial. Proceedings of the Royal Society of London, B: Biological Sciences 278:2768–2776.

Bartoń, K. 2020. MuMIn: multi-model inference. R package version 1.43.17. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf. Accessed 9 March 2020.

Belcher, C. A., and J. P. Darrant. 2006. Den use by the spotted-tailed quoll *Dasyurus maculatus* in south-eastern Australia. Australian Mammalogy 28:59–64.

Bonaparte, E. B., and K. L. Cockle. 2017. Nest niche overlap among the endangered Vinaceous-breasted Parrot (*Amazona vinacea*) and sympatric cavity-using birds, mammals, and social insects in the subtropical Atlantic Forest, Argentina. The Condor 119:58–72.

Breheny, P., and W. Burcheet. 2017. Visualisation of regression models using visreg. The R Journal 9:56–71.

Bunnell, F. L. 2013. Sustaining cavity-using species: patterns of cavity use and implications to forest management. ISRN Forestry 2013:457698.

Burbidge, A. A., and J. C. Z. Woinarski. 2016. *Conilurus penicillatus*. In: IUCN 2016. The IUCN Red List of Threatened Species. Version 2016.1. e.T5224A22450418. https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T5224A22450418.en. Accessed 9 March 2020.

Calenge, C. 2020. Package 'adehabitatHR'. R package version 0.4.18. https://cran.r-project.org/web/packages/adehabitatHR/adehabitatHR.pdf. Accessed 9 March 2020.

Carey, A. B., T. M. Wilson, C. C. Maguire, and B. L. Biswell. 1997. Dens of northern flying squirrels in the pacific northwest. Journal of Wildlife Management 61:684–699.

Carvalho, F., R. Carvalho, A. Mira, and P. Beja. 2014. Use of tree hollows by a Mediterranean forest carnivore. Forest Ecology and Management 315:54–62.

Christian, K., B. Green, G. Bedford, and K. Newgrain. 1996. Seasonal metabolism of a small, arboreal monitor lizard, *Varanus scalaris*, in tropical Australia. Journal of Zoology (London) 240:383–396.

Cockle, K., L. K. Martin, and M. C. Drever. 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biological Conservation 143:2851–2857.

Cockle, K., L. K. Martin, and T. Wesolowski. 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment 9:377–382.

Corey, B., I. J. Radford, A. N. Andersen, J. J. Perry, S. Legge, and J. C. Z. Woinarski. 2019. Better biodiversity accounting is needed to prevent bioperversity and maximize co-benefits from savanna burning. Conservation Letters 13:e12685.

Crane, M. J., D. B. Lindenmayer, and R. B. Cunningham. 2010. The use of den trees by the squirrel glider (*Petaurus norfolcensis*) in temperate Australian woodlands. Australian Journal of Zoology 58:39–49.

Davies, H. F., et al. 2018. Declining populations in one of the last refuges for threatened mammal species in northern Australia. Austral Ecology 43:602–612.

Davies, H. F., et al. 2017. Top-down control of species distributions: feral cats driving the regional extinction of a threatened rodent in northern Australia. Diversity and Distributions 23:272–283.

Edworthy, A. B., M. K. Trzcinski, K. L. Cockle, K. L. Wiebe, and K. Martin. 2018. Tree cavity occupancy by nesting vertebrates across cavity age. Journal of Wildlife Management 82:639–648.

Fairweather, A. A., R. E. Brockie, and G. D. Ward. 1987. Possums (*Trichosurus vulpecula*) sharing dens: a potential infection route for bovine tuberculosis. New Zealand Veterinary Journal 35:15–16.

Firth, R. S. C., B. W. Brook, J. C. Z. Woinarski, and D. A. Fordham. 2010. Decline and likely extinction of a northern Australian native rodent, the brush-tailed rabbit-rat *Conilurus penicillatus*. Biological Conservation 143:1193–1201.

Firth, R. S. C., E. Jefferys, J. C. Z. Woinarski, and R. A. Noske. 2005. The diet of the brush-tailed rabbit-rat (*Conilurus penicillatus*) from the monsoonal tropics of the Northern Territory, Australia. Wildlife Research 32:517–523.

Firth, R. S. C., J. C. Z. Woinarski, and K. G. Brennan. 2006a. Environmental relationships of the brush-tailed rabbit-rat, *Conilurus penicillatus*, and other small mammals on the Tiwi Islands, northern Australia. Journal of Biogeography 33:1820–1837.

Firth, R. S. C., J. C. Z. Woinarski, and R. A. Noske. 2006b. Home range and den characteristics of the brush-tailed rabbit-rat (*Conilurus penicillatus*) in the monsoonal tropics of the Northern Territory, Australia. Wildlife Research 33:397–407.

Fisher, D. O., et al. 2014. The current decline of tropical marsupials in Australia: is history repeating? Global Ecology and Biogeography 23:181–190.

Friend, G. R. 1987. Population ecology of *Mesembriomys gouldii* (Rodentia: Muridae) in the wet-dry tropics of the Northern Territory, Australia. Wildlife Research 14:293–303.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gibbons, P., and D. B. Lindenmayer. 2002. Tree hollow and wildlife conservation in Australia. CSIRO Publishing. Collingwood, Victoria, Australia.

Gibbons, P., D. B. Lindenmayer, S. C. Barry, and M. T. Tanton. 2002. Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. Biological Conservation 103:1–12.

Goldingay, R. L. 2011. Characteristics of tree hollows used by Australian arboreal and scansorial mammals. Australian Journal of Zoology 59:277–294.

Griffiths, A. D., J. Koenig, F. Carrol, and O. Price. 2002. Activity area and day-time tree use of the black footed tree-rat *Mesembriomys gouldii*. Australian Mammalogy 23:181–183.

Handasyde, K. A., and R. W. Martin. 1996. Field observations on the common striped possum (*Dactylopsila trivirgata*) in north Queensland. Wildlife Research 23:755–766.

Isaac, J. L. 2005. Life history and demographics of an island possum. Australian Journal of Zoology 53:195–203.

Isaac, J. L., J. L. De Gabriel, and B. A. Goodman. 2008. Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. Animal Conservation 11:281–287.

IUCN. 2019. The IUCN List of Threatened Species. www.iucnredlist.org. Accessed 20 February 2020.

Kerle, A. J. 1998. The population dynamics of a tropical possum, *Trichosurus vulpecula arnhemensis* Collett. Wildlife Research 25:171–181.

King, D., and B. Green. 1999. Goanna: the biology of varanid lizards. New South Wales University Press. Kensington, New South Wales, Australia.

Kobayashi, F., M. Toyama, and I. Koizumi. 2014. Potential resource competition between an invasive mammal and native birds: overlap in tree cavity preferences of feral raccoons and Ural owls. Biological Invasions 16:1453–1464.

Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy 71:641–653.

Leahy, L., et al. 2015. Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. Wildlife Research 42:705–716.

Legge, S. M., J. G. Smith, A. James, K. D. Tuft, T. Webb, and J. C. Z. Woinarski. 2019. Interactions among threats affect conservation management outcomes: livestock grazing removes the benefits of fire management for small mammals in Australian tropical savannas. Conservation Science Practice 1:1–13.

Lehmann, C. E., L. D. Prior, and D. M. Bowman. 2009. Fire controls population structure in four dominant tree species in a tropical savanna. Oecologia 161:505–515.

Liedloff, A. C., and G. D. Cook. 2007. Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the Flames simulation model. Ecology Modelling 201:269–282.

Lindenmayer, D. B., et al. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. Conservation Letters 7:61–69.

Lindenmayer, D. B., and R. B. Cunningham. 1997. Patterns of co-occurrence among arboreal marsupials in the forests of central Victoria, southeastern Australia. Austral Ecology 22:340–346.

Lindenmayer, D. B., R. B. Cunningham, and C. F. Connelly. 1997. Decay and collapse of trees with hollows in eastern Australian forests: impacts on arboreal marsupials. Ecological Applications 7:624–641.

Lindenmayer, D. B., R. B. Cunningham, M. T. Tanton, A. P. Smith, and H. A. Nix. 1990. The conservation of arboreal marsupials in the Montane ash forests of the central highlands of Victoria, Southeast Australia: I. Factors influencing the occupancy of trees with hollows. Biological Conservation 54:111–131.

Lindenmayer, D. B., W. F. Laurance, and J. F. Franklin. 2012. Ecology. Global decline in large old trees. Science 338:1305–1306.

Lindenmayer, D. B., and R. A. Meggs. 1996. Use of den trees by Leadbeater's possum (*Gymnobelideus leadbeateri*). Australian Journal of Zoology 44:625–638.

Marsden, S., and J. Pilgrim. 2003. Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests in New Britain, PNG. Ibis 145:45–53.

Matthews, S. M., D. S. Green, J. M. Higley, K. M. Rennie, C. M. Kelsey, and R. E. Green. 2019. Reproductive den selection and its consequences for fisher neonates, a cavity-obligate mustelid. Journal of Mammalogy 100:1305–1316.

McComb, L. B., et al. 2019. Feral cat predation on Leadbeater's possum (*Gymnobelideus leadbeateri*) and observations of arboreal hunting at nest boxes. Australian Mammalogy 41:262–265.

McGregor, H. W., H. B. Cliff, and J. Kanowski. 2016a. Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. Wildlife Research 43:623–633.

McGregor, H. W., S. Legge, M. E. Jones, and C. N. Johnson. 2016b. Extraterritorial hunting expeditions to intense fire scars by feral cats. Scientific Reports 6:22559.

Menkhorst, P. W. 1984. Use of nest boxes by forest vertebrates in Gippsland: acceptance, preference and demand. Wildlife Research 11:255–264.

Murphy, B. P., and H. F. Davies. 2014. There is a critical weight range for Australia's declining tropical mammals. Global Ecology and Biogeography 23:1058–1061.

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biologica 70:265–276.

Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15:167–175.

Oksanen, J., et al. 2019. vegan: community ecology package. R package version 2.5-6. https://cran.r-project.org/web/packages/vegan/vegan.pdf. Accessed 9 March 2020.

Penton, C. E., L. A. Woolley, I. R. Radford, and B. P. Murphy. 2020. Blocked-off: termitaria cause the overestimation of tree

hollow availability by ground-based surveys in northern Australia. Forest Ecology and Management 458:117707.

Pittman, G. 2003. Occurrence and use of tree hollows by mammals in fragmented and continuous savanna woodlands in Northern Australia. Honors thesis, Northern Territory University. Darwin, Northern Territory, Australia.

Prior, L. D., B. P. Murphy, and J. Russell-smith. 2009. Environmental and demographic correlates of tree recruitment and mortality in north Australian savannas. Forest Ecology and Management 257:66–74.

PWCNT [Parks and Wildlife Commission of the Northern Territory]. 1998. Sustainable use of wildlife. Pp. 212–237 in The history and natural resources of the Tiwi Islands Northern Territory. Prepared for the Tiwi Land Council. Darwin, Northern Territory. Australia.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/. Accessed 9 March 2020.

Remm, J., and A. Lõhmus. 2011. Tree cavities in forests – the broad distribution pattern of a keystone structure for biodiversity. Forest Ecology and Management 262:579–585.

Ruczynski, I., and W. Bogdanowicz. 2005. Roost cavity selection by Nyctalus noctula and N. leisleri (Vesperilionidae, Chiroptera) in Bialoweiza primeval forest, eastern Poland. Journal of Mammalogy 86:921–930.

Russell-smith, J., et al. 2003. Contemporary fire regimes of northern Australia, 1997–2001: change since Aboriginal occupancy, challenges for sustainable management. International Journal of Wildland Fire 12:283–297.

Russell-smith, J., et al. 2013. Managing fire regimes in north Australian savannas: applying Aboriginal approaches to contemporary global problems. Frontiers in Ecology and the Environment 11:55–63.

Sarà, M., A. Milazzo, W. Falletta, and E. Bellia. 2005. Exploitation competition between hole-nesters (Muscardinus avellanarius, Mammalia and Parus caeruleus, Aves) in Mediterranean woodlands. Journal of Zoology 265:347–357.

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.

Seryodkin, I. V., et al. 2003. Denning ecology of brown bears and Asiatic black bears in the Russian Far East. Ursus 14:153–161.

Shine, R. 1986. Food habits, habitats and reproductive biology of four sympatric species of varanid lizards in tropical Australia. Herpetologica 42:346–360.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Smith, G. C., M. Mathieson, and L. Hogan. 2007. Home range and habitat use of a low-density population of greater gliders, Petauroides volans (Pseudocheiridae: Marsupialia), in a hollow-limiting environment. Wildlife Research 34:472–483.

Soderquist, T. R. 1993. Maternal strategies of Phascogale tapoatafa (Marsupialia: Dasyuridae). I. Breeding seasonality and maternal investment. Australian Journal of Zoology 41:527–536.

Stobo-Wilson, A. M., B. P. Murphy, T. Cremona, and S. M. Carthew. 2019. Contrasting patterns of decline in two arboreal marsupials from Northern Australia. Biodiversity and Conservation 28:2951–2965.

Suzuki, K., M. Sagawa, and H. Yanagawa. 2013. Nest cavity selection by the Siberian flying squirrel Pteromys volans. Hystrix 24:187–189.

Taylor, R., J. C. Z. Woinarski, and R. Chatto. 2003. Hollow use by vertebrates in the Top End of the Northern Territory. Australian Journal of Zoology 32:462–476.

Traill, B. J., and A. Lill. 1997. Use of tree hollows by two sympatric gliding possums, the squirrel glider, Petaurus norfolcensis and the sugar glider, P. breviceps. Australian Mammalogy 20:79–88.

van der Hoek, Y., G. V. Gaona, and K. Martin. 2017. The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world. Diversity and Distributions 23:1120–1131.

van der Ree, R., A. F. Bennett, and T. R. Soderquist. 2006. Nest-tree selection by the threatened brush-tailed phascogale (Phascogale tapoatafa) (Marsupialia: Dasyuridae) in a highly fragmented agricultural landscape. Wildlife Research 33:113–119.

Whitford, K. 2002. Hollows in Jarrah (Eucalyptus marginata) and Marri (Corymbia calophylla) trees: I. Hollow sizes, tree attributes and ages'. Forest Ecology and Management 160:611–622.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag. New York.

Williams, R. J., G. D. Cook, A. M. Gill, and P. H. R. Moore. 1999. Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. Austral Ecology 24:50–59.

Woinarski, J. C. Z., et al. 2010. Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park - northern Australia. Wildlife Research 37:116–126.

Woinarski, J. C. Z., et al. 2011. The disappearing mammal fauna of northern Australia: context, cause, and response. Conservation Letters 4:192–201.

Woinarski, J. C. Z., K. G. Brennan, I. Cowie, R. Kerrigan, and C. Hempel. 2003. Summary. Pp. i–ii in Biodiversity conservation on the Tiwi Islands, Northern Territory. Prepared for the Northern Territory Government Department of Infrastructure, Planning and Environment and the Tiwi Land Council. Darwin, Northern Territory, Australia.

Woinarksi, J. C. Z., and A. A. Burbidge. 2016. Mesembriomys gouldii. In: The IUCN Red List of Threatened Species 2016. Version 2016.1. e.T13211A22448856. https://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T13211A22448856.en. Accessed 9 March 2020.

Woinarksi, J. C. Z., A. A. Burbidge, and P. Harrison. 2014. Action plan for Australian mammals 2012. CSIRO Publishing. Melbourne, Victoria, Australia.

Woolley, L. A., B. P. Murphy, I. J. Radford, J. Westaway, and J. C. Z. Woinarksi. 2018. Cyclones, fire, and termites: the drivers of tree hollow abundance in northern Australia's mesic tropical savanna. Forest Ecology and Management 420:146–159.

Ziembicki, M. R., et al. 2015. Stemming the tide: progress towards resolving the causes of decline and implementing management responses for the disappearing mammal fauna of northern Australia. Therya 6:169–225.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.