Illuminating den-tree selection by an arboreal mammal using terrestrial laser scanning in northern Australia

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Abstract
There has been a significant decline in arboreal mammals in northern Australia, especially in the lower rainfall region of the tropical savannas. Currently, we lack a fundamental understanding of the habitat requirements of these species to prevent further declines. We investigated how variation in habitat structure influences den-tree selection by an arboreal, hollow-dwelling marsupial, the savanna glider (\textit{Petaurus ariel}; Gould, 1842), in northern Australia from two populations at the climatic extremes of the species’ geographic range. We used traditional habitat surveys complemented by advanced terrestrial Light Detection And Ranging (LiDAR) technology to compare site habitat structure and subsequent den-tree selection by \textit{P. ariel}. Canopy height, total canopy cover and tree size were positively correlated with rainfall. At the higher rainfall site, \textit{P. ariel} selected larger trees for denning than neighbouring trees; mean trunk diameter at breast height was 53.4 cm (95% CI: 49.6–56.8) and 33.8 cm (95% CI: 30.0–37.6), for den and neighbouring trees respectively. At the lower rainfall site, \textit{P. ariel} den trees were no larger than neighbouring trees but were more likely to be \textit{Eucalyptus tectifica} than any other available tree species. At both sites, \textit{P. ariel} selected den trees that were more likely to be hollow bearing (through larger tree size or specific tree species). We found terrestrial LiDAR to be a useful tool for mapping fine-scale variation in habitat structure which enabled us to account for variation in den-tree selection between sites. However, we remained dependent on traditional habitat surveys to count hollows and identify tree species. With a better understanding of the relationship between tree size and den-tree selection, future studies could use terrestrial LiDAR to map the probability of den-tree availability for hollow-dwelling species at a landscape scale. We emphasize the importance of protecting hollow-bearing eucalypt trees for the conservation of arboreal mammals in northern Australia.

Introduction
Habitat modification (e.g. logging and vegetation clearing) and alteration of ecosystem processes (e.g. intensification of disturbance regimes) by humans have caused global declines in biodiversity (Ceballos et al. 2015). Human-driven declines in the abundance of large, hollow-bearing trees (Cockle et al. 2011; Lindenmayer et al. 2012; Lindenmayer et al. 2013) have been particularly detrimental to hollow-dependent fauna, including many arboreal mammals (Lindenmayer 2000; Wayne et al. 2006; Lampila et al. 2009). Due to the longtime periods required for tree hollows to form, conservation efforts are best targeted at identifying and protecting these critical resources for arboreal mammals and other hollow-dependent species (Fisher and Wilkinson 2005; Lindenmayer et al. 2014). Thus, considerable research effort has been spent determining the fine-scale habitat requirements of arboreal mammals, particularly their den-tree requirements (Hanski et al. 2000; Goldingay 2011; Lindenmayer et al. 2017).

The last 200 years has seen an exceptionally high rate of extinction of Australia’s native mammal fauna (Short...
and Smith 1994; McKenzie et al. 2007; Woinarski et al. 2015). Mammal declines in northern Australia’s tropical savannas are the most recently recorded declines on the continent (Woinarski et al. 2010). Of those mammals that have experienced marked declines in northern Australia, the majority are semi-arboreal and arboreal (Fitzsimons et al. 2010), and are to some extent hollow dependent (Griffiths et al. 2001; Firth et al. 2006). For many species, declines first occurred in more southerly areas of lower rainfall, with a gradual and continuing contraction to the northern mesic ends of the species’ former range (Firth et al. 2010; Start et al. 2012). There is a strong rainfall gradient in the tropical savannas, with areas of high rainfall having greater tree species richness, tree height, canopy cover and basal area relative to areas of low rainfall (Williams et al. 1996). Hollow abundance (defined as the number of distinguishable external entrances to internal tree cavities) also decreases with decreasing rainfall and is likely to be declining under current fire regimes (more frequent, high-intensity fires; Woolley et al. 2018). A review on tree-hollow use by Australian arboreal mammals demonstrated a strong positive correlation between the abundance of hollow-dwelling species and hollow availability (Goldingay 2011). Thus, it is plausible that declines in arboreal mammals in the tropical savannas of northern Australia may in part be the result of reduced hollow availability, especially in areas of lower rainfall due to altered fire regimes.

Despite considerable research effort detailing fine-scale attributes of the den trees used by arboreal mammals in south-eastern Australia (Lindenmayer and Meggs 1996; Rowston 1998; Jackson 2000), only two studies have described use and selection of den trees by arboreal mammals in the tropical savannas of northern Australia (Griffiths et al. 2001; Firth et al. 2006). Both studies highlighted a preference for larger eucalypt species as den trees, but due to their localized scale provide little insight on how arboreal mammal habitat use varies with the rainfall gradient in the tropical savannas. The continuing decline in arboreal mammals in northern Australia has highlighted a significant knowledge gap in the fine-scale habitat requirements of arboreal mammals in the tropical savannas.

There has been a recent increase in cross-disciplinary studies that combine remote-sensing technologies, which characterize fine-scale habitat structure and availability, with behavioural and habitat use observations to determine the habitat requirements of species (Squires et al. 2013; Davies and Asner 2014; McLean et al. 2016). Light detection and ranging (LiDAR) technology provides an alternative and effective method for ecologists to capture subtle variation in habitat structure, especially three-dimensional forest structure, over a large area (Lefsky et al. 2002; Hudak et al. 2009). LiDAR sensors can operate from multiple platforms (Beland et al. 2019), including airborne LiDAR (e.g. airplane or drone based) and terrestrial laser scanning (TLS; e.g. vehicle and ground based). Trade-offs between the different platforms dictate which platform is most appropriate for the intended application. For example, TLS provides greater density point clouds of local targets (e.g. individual trees) which offers greater spatial resolution for 3D characterization, but is limited in geographic spatial extent. Alternatively, airborne LiDAR will cover a greater geographic spatial extent for landscape-scale surveys but with lower point cloud density and restricted resolution of the lower canopy and ground cover (see Beland et al. 2019 for a detailed review on the applicability of multiple LiDAR platforms for forest ecosystem research).

By capturing measures of canopy structure that were previously unmeasurable or required considerable effort to capture using traditional field measurement methods, LiDAR can improve our understanding of fine-scale habitat selection by arboreal mammals (McLean et al. 2016; Blakey et al. 2017; Davies et al. 2017a; Davies et al. 2019). For example, Davies et al. (2017a, 2019) used airborne LiDAR to illustrate how structural attributes of the upper forest canopy (i.e. increased canopy cover and uniform canopy height) were important for movement by the large-bodied Bornean orangutan (Pongo pygmaeus). Blakey et al. (2017) used TLS to capture elements of the lower canopy structure which could be linked to the foraging strategy of three different bat species. Despite the importance of den trees for a range of arboreal mammals, LiDAR has not yet been used to determine fine-scale den-tree selection by a hollow-dependent arboreal mammal. However, LiDAR may be a useful avenue for mapping den-tree availability for hollow-dwelling species, and provide alternative metrics to model den-tree availability. Specifically, TLS could be used to capture fine-scale tree variation to model den-tree selection as this platform provides the highest level of spatial detail in the form of 3D point clouds that approximate reality.

As a step towards understanding the cause of regional arboreal mammal decline in northern Australia (i.e. plausibility of hollow abundance as a contributing factor), we investigated how variation in habitat structure influences den-tree selection by an arboreal, hollow-dwelling marsupial. Our study species was the recently described savanna glider (Petaurus ariel; Gould, 1842), which has declined in the lower rainfall parts of its range (Stobo-Wilson et al. 2019). The aim of this study was to use a novel technology to describe den-tree selection of P. ariel in northern Australia. Our core objectives were to: i) quantify how variation in habitat structure and composition (e.g. tree size, canopy size, hollow abundance and species richness)
influences den-tree selection by *P. ariel* at either end of the species’ geographic range; and ii) assess the feasibility of using TLS, relative to field-based habitat surveys, to model den-tree selection and potentially den-tree availability in future studies.

### Materials and Methods

#### Study species

*Petaurus ariel* is an obligate hollow-denning arboreal marsupial (65–140 g; Cremona et al. 2020). Although previously listed as *P. breviceps* subsp. *riel* (Malekian et al. 2010), the species has recently been taxonomically reclassified and elevated to species level (Cremona et al. 2020). *Petaurus ariel* occurs exclusively in the tropical savannas of northern Australia. *Petaurus ariel* belongs to the Petauridae family, the species’ patagium enables it to glide between trees and stay in the canopy layer, therefore spending little time on the ground (Jackson 2012). Petaurid gliders have a primarily exudivorous and insectivorous diet (Goldingay and Jackson 2004). Until recently, *P. ariel* was anecdotally believed to be the only widespread savanna mammal within the so-called ‘critical weight range’ that had not declined within northern Australia (Woinarski et al. 2010; Woinarski et al. 2014). The ‘critical weight range’ refers to Australian native mammals with body mass 35–5500 g that are highly susceptible to decline and extinction (Burridge and McKenzie 1989).

However, analysis of the contemporary distribution of *P. ariel* has found evidence of moderate decline in the southern (lower rainfall) end of its distribution (Stobo-Wilson et al. 2019), although the extent of decline has been far less severe than that of other arboreal mammals.

### Study region and site selection

This study took place in the fire-prone tropical savannas of northern Australia (Fig. 1). The tropical savannas are north of the 500 mm isohyet and comprise one of the world’s largest remaining expanses of tropical savanna, covering an estimated 1.9 million km² (Bradshaw 2012). The region is characterized by a distinct wet season (December-April), which encompasses almost all (>90 %) of the year’s rainfall, and an almost rainless dry season (May-November), which coincides with the region’s fire season. The tropical savannas are typically dominated by eucalypts (*Eucalyptus* and *Corymbia* spp.; Williams et al. 1996), which are an important source of tree hollows for fauna in northern Australia (Woolley et al. 2018), and Australia more broadly (Gibbons et al. 2002; Goldingay 2011). The primary drivers of eucalypt tree-hollow formation in northern Australia are cyclones, fire and termites, with a greater probability of tree hollows forming in larger and taller trees (Woolley et al. 2018).

To determine how variation in habitat structure and composition influences den-tree selection by *P. ariel*, we established a population monitoring site at either end of the species’ geographic range; one site at the northern end of the species’ range, located on Melville Island (Fig. 1) where mean annual rainfall is relatively high (1695 mm), and a second site at the southern end of the species’ range within Nitmiluk National Park, where rainfall is relatively low (1074 mm). A comparison of broad environmental characteristics between the two study sites is given in Table 1. We note that we have not controlled for variation in fire regime between our study sites, however, within the tropical savannas, areas of higher rainfall typically have greater fire frequency but lower fire intensity, relative to areas of low rainfall (Murphy et al. 2019).

In addition, there was a discrepancy in the size of our two population monitoring sites, the high rainfall site covered an area much smaller (~0.05 km²) than that of the low rainfall site (~ 0.40 km²). The difference in the size of our sites was necessary to compensate for lower density of *P. ariel* at the low rainfall site (Stobo-Wilson et al. 2019), and ensured that a similar number of individuals could be monitored at each site.

#### Radio-tracking and field-based habitat surveys

During the dry seasons (May–November) of 2016 and 2017, we set 40-50 Elliott (aluminium box) traps each night for up to 20 nights at each site. Traps were placed at 20–50 m intervals, 4–5 m above ground level. All traps were strapped to a bracket using tape. The brackets were secured to each tree with nails and the traps positioned there with a 10 cm gap between the tree trunk and the trap entrance. We baited traps with a mixture of peanut butter, honey and rolled oats. We sprayed a solution of honey and water (ratio 1:5) along the tree trunk above the trap. Animals were removed from traps at first light each morning, processed and held in calico bags until release. We fitted gliders with a single-stage brass-loop radio-transmitter collar weighing 3.2 g (Sirtrack, Hawkes Bay, New Zealand). Animals were released at the point of capture, either within an hour of capture or at last light that evening.

In total, we radio-collared 17 adult gliders (11 males; 7 females) at the high rainfall site (8 in 2016; 10 in 2017) and 8 adult gliders (4 males; 4 females) at the low rainfall site (3 in 2016; 5 in 2017). We used a hand-held antenna and Ultra Receiver (Sirtrack, Hawkes Bay, New Zealand) to track gliders. Den-tree locations were recorded daily for all individuals from the day after release until collars.
were removed (10–45 days and 8–28 days after capture at the high and low rainfall sites respectively). For each recorded den tree, we recorded the diameter at breast height (130 cm above ground; DBH), tree height (using a laser rangefinder with a built-in clinometer), species, whether the tree was alive or dead and number of visible hollows (i.e. entrance to tree cavities; minimum entrance diameter $\geq$ 5 cm, Goldingay 2011). We additionally recorded the species, DBH, height, whether the tree was alive or dead and number of visible hollows of all trees ($\geq$ 5 cm DBH) within 12 quadrats (10 m x 10 m) at each site (taken from the area in which radio-locations were recorded).

Terrestrial laser scanning

Study site scanning

We used a Riegl VZ-2000 terrestrial laser scanner (RIEGL Laser Measurement Systems GmbH) mounted on a motor vehicle, to capture the three-dimensional structure of vegetation in both study sites. We completed 45 and 30 scans at the high and low rainfall sites, respectively, with scans spaced 25 m apart along a straight-line transect. Although covering a smaller area, more scans were required at the high rainfall site to reduce occlusion and compensate for greater vegetation density. Scans were taken within the

Table 1. Environmental characteristics of the two study sites within the tropical savannas of the Northern Territory where Petaurus ariel individuals were radio-tracked between 2016 and 2017.

| Location               | Minimum daily temperature ($^\circ$C) | Maximum daily temperature ($^\circ$C) | Number years burnt (2000-2017) | Mean annual rainfall (mm) | Mean tree density (ha$^{-1}$)$^1$ | Live tree basal area (m$^2$ ha$^{-1}$)$^*$ | Net primary productivity (t C ha$^{-1}$ year$^{-1}$) |
|------------------------|--------------------------------------|--------------------------------------|-------------------------------|---------------------------|----------------------------------|------------------------------------------|-----------------------------------------------|
| Melville Island        | 22                                   | 31                                   | 5                             | 1695                      | 891.7                            | 16.6                                     | 11.5                                           |
| -11.40°; 130.58°       |                                       |                                      |                               |                           |                                  |                                          |                                                |
| Nitmiluk National Park | 20                                   | 33                                   | 8                             | 1074                      | 521.4                            | 12.6                                     | 3.4                                            |
| -14.15°; 132.20°       |                                       |                                      |                               |                           |                                  |                                          |                                                |

$^1$Based on trees with a diameter at breast height $> 5$ cm

Figure 1. Locations of study sites in the Northern Territory; solid black lines indicate mean annual rainfall isohyets. Square inset shows location of study region relative to Australia and the contemporary distribution of Petaurus ariel (shaded grey; Stobo-Wilson et al., 2019).
same survey period as radio-tracking and habitat surveys. The scanner was operated at 550 kHz with an angular sampling step of 0.02 mrad. We integrated a Leica GS16 RTK GNSS system with the laser scanner to obtain high positional accuracy. Individual scans were co-registered using the Multi-station Adjustment Module (ICP based) embedded in Rieg1's RiSCAN PRO software. Co-registered scans were merged, filtered for noise and thinned with a 0.02 m octree filter prior to export in.las format in UTM52S for further analysis (Fig. 2).

Structural characteristics of each study landscape
From the merged TLS point cloud, we used stratified sampling plots to explore the variation in vegetation structural characteristics of each study site. We generated uniformly spaced circular polygons of 40 m diameter (sampling plots) to clip the point cloud of each study site – deriving 80 plots at the high rainfall site and 90 plots at the low rainfall site. We generated TLS-derived metrics from the point cloud of each plot using the 'lascanopy' scripts within LAStools (Isenburg 2014). We compared the canopy structure of the stratified survey plots by calculating the frequency of points for every 1 m in height from 1 to 35 m (generated from total point density; Fig. 3), and calculating canopy cover for each plot.

Individual den and neighbour tree structural analysis
We identified the location of the den trees in the point cloud of each study site using the GPS locations recorded during radio-tracking. Once the den tree was identified, three neighbouring trees were selected from the point cloud. Neighbouring trees were classified as the largest trees within 30 m from a den tree. This selection process meant neighbouring trees were likely to be hollow bearing and accessible to the glider, and were therefore more informative for comparison against den trees. From the merged TLS point clouds, we then clipped a 20m-diameter plot at the location of each den and neighbouring tree. Using LAStools (Isenburg 2014), we classified the ground returns and standardized (otherwise referred to as normalized) the point clouds to elevation above ground level. We then manually cropped each den and neighbouring tree from their respective plot point clouds using Quick Terrain Modeler (Applied Imagery, 2017) (Fig. 2e, f). We manually cropped den and neighbouring trees from the plots (as opposed to the study site point cloud) to reduce the computational requirement of having to reload the study site point cloud when cropping each tree. This step substantially reduced the overall time taken to crop individual trees.

To compare the canopy height structure of den and neighbouring trees, using LAStools (Isenburg 2014), we calculated the point density for every 1 m in height from 1 to 35 m from the cropped den and neighbouring tree point clouds. To model den-tree selection by P. ariel, we generated 13 TLS-derived measures of tree structure using the free online software SAGA GIS (Conrad et al. 2015), 3D Forest (Trochta et al. 2017) and CloudCompare (GPL software, 2018) (Table 2). Twenty-four of the recorded den trees could not be characterized using TLS as they either fell outside of the scanned area or the point clouds of the individual trees were not of high enough quality (due to occlusion artefacts) to generate reliable metrics.

Statistical analyses
All analyses were conducted in R (R Development Core Team, 2017). We used a Kruskal–Wallis test (Breslow 1970) to determine differences in canopy structure (canopy height and canopy cover) between areas of high and low rainfall, using TLS-derived metrics from the stratified survey plots. We also used a Kruskal–Wallis test to determine if tree attributes (DBH, maximum canopy diameter and tree height) significantly varied between areas of high and low rainfall. For this we used TLS-derived measures of tree structure generated from den and neighbour trees at each site. Using an ordinary least-squares linear model, we modelled the relationship between tree height and canopy diameter against DBH at both the high and low rainfall study sites. We used Akaike’s Information Criterion (AIC) to select the most parsimonious model in the candidate set (Burnham and Anderson 2003). The model with the lowest AIC score by ≥ 2 AIC units was deemed the top model for predicting tree structure between the two study sites.

We used Pearson’s chi-squared test (Garson and Moser 1995) to determine if P. ariel preferentially selected particular tree species for denning relative to what was available in the area. Within each site, we calculated ‘expected’ species richness of den trees from the field-based habitat surveys and compared that against the ‘observed’ species richness of den trees for the site. For each study site, we created a dataset that combined the field-based quadrat habitat surveys with field-collected den-tree measurements (as both datasets identified tree species and hollow abundance). With this, we modelled mean hollow abundance as a function of tree species, site and DBH using a negative-binomial generalized linear model (GLM) from the ‘MASS’ package (Venables and Ripley 2002) in R. We used AIC to rank models (Burnham and Anderson 2003). The model with the lowest AIC score by ≥ 2 AIC units was deemed the top model for predicting hollow abundance.
To model den-tree selection by *P. ariel*, we used a GLM with a binomial distribution. Each model had a binary response of ‘den’ (1) or ‘neighbour’ (0). We modelled all 13 LiDAR-derived measures of tree structure as predictors of den-tree selection. Given that many predictor variables were strongly correlated ($r > 0.7$), we used two approaches to analyse the dataset. We first ran a multivariate model including only predictor variables that were not strongly correlated. Here, we used a model averaging approach to identify important predictor variables (relative variable importance ≥ 0.73; Grueber et al., 2011), using the ‘MuMIn’ package (Bartín 2013). Secondly, we modelled all measures of tree size (13 variables) in separate models to determine the single best predictor of den-tree selection. The model with the lowest AIC in the candidate set (by > 2 AIC-units) was deemed the best model. For all relevant analyses, we used the log of DBH, as it improved model fit and has previously been found to be a better predictor of hollow abundance (Rayner et al. 2014). Prior to analyses, predictor variables were centred and standardized.

**Results**

We found a strong correlation between TLS-derived estimates of DBH and field-measured values ($R^2 = 0.87$; RMSE = 5.59). The slope of the regression of TLS-derived DBH against field-derived DBH was 0.96 (with 95% confidence intervals overlapping 1), and the intercept was 2.5 (with 95% confidence intervals overlapping 0; Fig. 4). This gave us good confidence in the use of the TLS data for DBH measurements and, hereafter, report only TLS-derived values of DBH for both den and neighbour trees.

**Study site habitat structure**

From field-based habitat surveys, we recorded similar richness in tree species at both the high and low rainfall study sites. Within the 12 surveyed quadrats at the high rainfall site we recorded eight different tree species from a total of 99 trees, and at the low rainfall site we recorded six different tree species from 53 trees. There was substantially greater tree abundance (count of trees with DBH ≥ 5 cm) at the high rainfall site (mean: 8.8 trees per ha; 95% CI: 7.220–10.446) than the low rainfall site (mean: 4.6 trees per ha; 95% CI: 3.361–5.839). Only two species occurred at both sites (*Erythrophleum chlorostachys* and *Terminalia ferdinandiana*). Eucalypts were more dominant than non-eucalypts at the high rainfall site (75.5% of trees were eucalypts; $\chi^2 = 37.586$, df = 1, $p < 0.001$), but not at the low rainfall site (40.5% of trees were eucalypts; $\chi^2 = 1.324$, df = 1, $p < 0.250$). At the low rainfall site, *Er. chlorostachys* was the most abundant tree species (51.4% of trees, cf. 7.1% of trees at the high rainfall site).

Figure 2. Comparison of vegetation structure at the high (A, C and E) and low (B, D and F) rainfall sites, including examples of terrestrial LiDAR scans from each site (C, D) and den trees clipped from LiDAR point clouds (E, F). Note that the trees visible in (A) and (B) differ markedly in height: ≤29.8 m in (A) and ≤ 14.4 m in (B).
Analyses of TLS-derived metrics from survey plots showed a significantly taller canopy layer and greater canopy cover at the high rainfall site, compared to the low rainfall site (Table 3). Trees were substantially larger at the high rainfall site than the low rainfall site (Fig. 3a). TLS-derived measures of DBH, maximum canopy diameter and tree height were all significantly greater at the high rainfall site than the low rainfall site (Table 3). In addition, trees of a given DBH at the high rainfall site (standardized beta coefficient \( \beta \): 'log 10 DBH site' 4.65 \pm 1.11, \( p < 0.001 \)) were substantially taller than trees of the same DBH at the low rainfall site (ordinary least-squares linear model, Table 4; Fig. 5); the same was not true for canopy size ('log 10 DBH site' 1.40 \pm 1.07, \( p < 0.195 \)). There was also greater variability in tree size (DBH, maximum canopy diameter and height) at the high rainfall site than the low rainfall site (Table 3).

### Den-tree selection by *P. ariel*

We recorded dens being used on 457 occasions at the high rainfall site and 147 occasions at the low rainfall site. Most individuals used multiple den trees (1 to 9 dens per individual). In total, we identified and collected field measurements from 74 den trees; 48 from the high rainfall site and 26 from the low rainfall site. At both study sites, only eucalypt species and *Er. chlorostachys* were used as den trees by *P. ariel*. At the low rainfall site, fewer tree species than were available in the area (6 hollow-forming tree species) were used as den trees (4 species) (\( x^2 = 16.924, df = 5, P = 0.024 \)). Relative to availability, *P. ariel* selected more *Eu. tectifica* (\( x^2 = 3.591, df = 1, P = 0.003 \)) and fewer dead trees (\( x^2 = 2.168, df = 1, P = 0.025 \)) as den trees. In contrast, at the high rainfall site there was no difference in the number of tree species used as den trees (6 hollow-forming tree species) and the number of tree species at the site (5 species) (\( x^2 = 7.161, df = 5, P = 0.291 \)).

We were able to generate TLS-derived measures of tree size for 25 den trees and 67 neighbouring trees at the high rainfall site, and 25 den trees and 46 neighbouring trees at the low rainfall site. From these measures of tree size, we found evidence of size-based den-tree selection by *P. ariel* (Fig. 6). Model averaging demonstrated that...
Table 2. Terrestrial LiDAR-derived measures of tree structure generated from point clouds of den and neighbouring trees, used for modelling fine-scale den selection by *Petaurus ariel* at the high and low rainfall study sites in northern Australia. All measures were generated using free online software, including SAGA GIS (Conrad et al. 2015), 3D Forest (Trochta et al. 2017) and CloudCompare (GPL software, 2018).

| Predictor variable                                | Description and source                                                                 | Mean ± SE Low rainfall site | Mean ± SE High rainfall site |
|---------------------------------------------------|----------------------------------------------------------------------------------------|----------------------------|------------------------------|
| Tree height (m)                                   | Height of entire tree¹                                                                  | 11.09 ± 0.23               | 21.06 ± 0.47                 |
| Canopy height (m)                                 | Measure of crown from crown base to top of crown¹                                      | 8.39 ± 1.74                | 10.80 ± 0.37                 |
| Canopy surface area (concave hull) (m²)           | Surface area of 3D concave hull of the crown¹                                           | 206.46 ± 12.94             | 374.43 ± 24.11               |
| Canopy surface area (convex hull) (m²)            | Surface area of 3D convex hull of the crown¹                                            | 203.85 ± 16.93             | 496.11 ± 39.12               |
| Canopy volume (concave hull) (m³)                 | Volume of 3D concave hull of the crown¹                                                | 1059.15 ± 49.45            | 281.18 ± 21.96               |
| Canopy volume (convex hull) (m³)                  | 3D Forest metric: volume of 3D convex hull of the crown¹                                | 179.72 ± 10.16             | 323.32 ± 17.50               |
| Diameter at breast height (cm)                    | Diameter of tree at 1.3 m using ‘point picking’ tool in Cloud Compare                   | 28.63 ± 7.07               | 39.11 ± 1.64                 |
| Canopy area (m²)                                  | Area of polygon encompassing crown from birds-eye-view²                                | 37.27 ± 2.27               | 60.47 ± 3.54                 |
| Maximum canopy diameter (m)                       | Maximum distance across polygon encompassing crown from birds-eye-view²                 | 9.42 ± 0.32                | 11.30 ± 0.36                 |
| Canopy perimeter (m)                              | Perimeter of polygon encompassing crown from birds-eye-view²                           | 64.22 ± 3.16               | 72.71 ± 4.94                 |
| Canopy perimeter (m) / area (m²)                  | Perimeter of polygon encompassing crown from birds-eye-view, divided by area of polygon² | 1.88 ± 0.08                | 1.31 ± 0.06                  |
| Canopy shape                                      | Shape index of polygon encompassing crown from birds-eye-view; lower values indicate a more circular shape² | 2.97 ± 0.87                | 2.60 ± 0.12                  |

¹Metric generated using 3D Forest software.  
²Metric generated using SAGA software.

...an interaction between site and DBH was the best predictor of den-tree selection by *P. ariel* (Table 5). At the high rainfall site, den-tree selection increased with increasing DBH (standardized beta coefficient ± standard error: ‘log₁₀ DBH × site’ 2.89 ± 1.20, *p* < 0.016).

...We integrated field-based habitat surveys and TLS technology to quantify habitat structure and characterize den-tree selection by *P. ariel* in northern Australia. We found greater tree abundance, canopy cover and variation in tree size (DBH, height and canopy diameter) at the high rainfall site, relative to the low rainfall site (Table 3). In addition, we found variation in den-tree use by *P. ariel* at each site (Table 5). At the high rainfall site, *P. ariel* selected den trees with a larger DBH than neighbouring trees (Fig. 6). However, at the low rainfall site there was no similar preference for den trees with a larger DBH.
Rather, *P. ariel* favoured *Eu. tectifica* as den trees, a species only recorded at the low rainfall site. We found trees with a larger DBH and *Eu. tectifica* trees were more likely to be hollow bearing (Table 6). Thus, at both sites *P. ariel* selected den trees that were more likely to be hollow bearing, which itself varied with habitat availability at each site (greater abundance of larger trees at the high rainfall site and more hollow-bearing tree species at the low rainfall site). Despite significant variation in habitat structure, our study highlights that hollow-bearing

![Figure 4](image-url). Comparison of field-based measures and LiDAR-derived values of diameter at breast height (DBH; cm) collected from den trees across both study sites. Regression line is shown in black, 1:1 line is indicated with a dashed red line shows the accuracy of the regression and grey band represents 95% confidence intervals.

![Table 3](table-url). Comparison of the height of the canopy layer and per cent of canopy cover taken from randomly generated survey plots at the high and low rainfall site; and tree size (including canopy size) of cropped den and neighbour trees (combined) at the high and low rainfall site.

We tested for significant variation between the two sites using a Kruskal–Wallis test and report values here; *H* is the Kruskal–Wallis statistic and df is degrees of freedom.

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Table 4. Model selection results for ordinary least-squares linear models of tree height and maximum canopy diameter, as a function of diameter at breast height (DBH) and site. Data were derived from the combined dataset of den and neighbouring trees at each site. ΔAIC represents the difference between the model’s AIC (Akaike’s Information Criterion) value and that of the top-ranking model; \( w_i \) is the Akaike weight. Bold text indicates the most supported models (ΔAIC ≤ 2).

| Response variable       | Model            | ΔAIC | \( w_i \) | \( R^2 \) |
|------------------------|------------------|------|----------|---------|
| Tree height            | \( \log_{10} \text{DBH} \times \text{Site} \) | 0.00 | 1.00     | 0.86    |
| Tree height            | \( \log_{10} \text{DBH} + \text{Site} \) | 15.12| 0.00     | 0.84    |
| Tree height            | \( \text{DBH} \) | 139.93| 0.00    | 0.66    |
| Tree height            | \( \text{DBH} \) | 214.27| 0.00    | 0.47    |
| Maximum canopy diameter| \( \log_{10} \text{DBH} \) | 0.00 | 0.44     | 0.52    |
| Maximum canopy diameter| \( \log_{10} \text{DBH} + \text{Site} \) | 0.76 | 0.30     | 0.52    |
| Maximum canopy diameter| \( \log_{10} \text{DBH} \times \text{Site} \) | 1.03 | 0.26     | 0.52    |
| Maximum canopy diameter| \( \text{Site} \) | 104.11| 0.00    | 0.10    |

eucalypts (typically larger trees or species that readily form hollows) are a critical resource for hollow-dwelling arboreal mammals across the tropical savannas of northern Australia. However, den-tree availability is likely to be limited in areas of lower rainfall as there is a smaller proportion of large eucalypt trees and relatively low tree abundance.

Capturing the 3D complexity of ecosystems with TLS

To accurately capture variation in habitat structure, our study complemented conventional field-based habitat surveys with TLS. By using TLS, we could quickly capture 10 structural attributes of the canopy that would have otherwise been too laborious, as well as conventional measures typically used in den tree studies (i.e. tree height and DBH). Of all possible predictors, DBH was the best predictor of den-tree selection by *P. ariel*. This is consistent with previous studies on den-tree selection by arboreal mammals (Meyer et al. 2005; Goldingay 2011; Lindenmayer et al. 2017). Incorporating TLS in this study allowed us to model (and subsequently eliminate) canopy structural elements previously poorly represented in den-tree selection studies. However, essential features such as tree species and hollow counts could not be confidently identified from our TLS analyses, so field-based habitat surveys were still necessary. Given the cost of TLS equipment (and other forms of LiDAR) and the computation effort required to generate the required metrics for modelling den-tree selection, TLS did not provide a cost-effective alternative to field-based habitat surveys in this instance.

Further investigation of the relationship among DBH, canopy size and hollow abundance might provide future pathways for large-scale mapping of den availability using terrestrial or airborne LiDAR. Indeed, airborne LiDAR has already been found to be a promising tool for modelling pathways of movement by arboreal mammals (Davies et al. 2017a; Davies et al. 2019), but few studies have explored the potential for TLS in this realm (Blakey et al. 2017). Another advantage of TLS in future studies of den-tree selection will be to monitor and quantify den-tree attrition over time, and in response to individual or repeated disturbances. For example, in northern Australia, TLS could enable better quantification of the loss of large (likely hollow-bearing) trees with different fire regimes, which can then be used to predict future den-tree availability for hollow-dwelling species. Our poor understanding of the drivers of den-tree attrition severely limits our ability to predict future hollow availability for arboreal mammals in northern Australia, and Australia more broadly (Goldingay 2011).

Den-tree selection and habitat use by arboreal mammals in northern Australia

Previous studies on arboreal mammal den use in northern Australia found both the brush-tailed rabbit-rat (*Conillurus penicillatus*; Firth et al., 2006) and black-footed tree-rat (*Mesembrinomys gouldii*; Griffiths et al., 2001) also used large, eucalypt trees for denning. Our findings suggest this preference is most likely driven by hollow availability, highlighting the importance of hollow-bearing eucalypt trees for declining arboreal mammal populations in northern Australia. There is some evidence that hollow-bearing eucalypts are decreasing in abundance from elevated frequency of high-intensity fires in northern Australia, relative to the historical baseline (Russell-Smith et al. 2007). Previous studies in northern Australia have found old eucalypts are particularly vulnerable to high-intensity fires (Williams et al. 1999), reducing hollow abundance in areas characterized by frequent high-intensity fires (Woolley et al. 2018). The impact of high-intensity fires on hollow-bearing eucalypts is also possibly more pronounced in areas of low rainfall where trees are typically shorter and water stressed and therefore more likely to be killed and consumed by fire (Midgley et al. 2010; Russell-Smith et al. 2010; Cook et al. 2015). This interaction between altered fire regimes and habitat structure in the tropical savannas may have caused a greater decline in hollow availability in areas of low rainfall. Furthermore, as tree abundance, and consequently hollow
abundance, declines with rainfall (Woolley et al. 2018), the loss of hollow-bearing eucalypts may be more ecologically significant in areas of low rainfall.

From our study it is not possible to determine whether tree hollows are a limiting resource in northern Australian savannas. However, from the results of this study in relation to *P. ariel* den-tree selection, we suggest a decline in tree hollow availability is unlikely to fully explain the disproportionate decline in arboreal mammals throughout the region. When comparing the severity of decline between arboreal mammals in northern Australia, both *C. penicillatus* and *M. gouldii* (Firth et al. 2010; Woinarski et al. 2010; Davies et al. 2018) have experienced more marked declines than *P. ariel* (Stobo-Wilson et al. 2019). However, we found that at the high rainfall site, *P. ariel* used den trees that were similar in size to that used by *C. penicillatus* and *M. gouldii* (also at high-rainfall sites). Mean DBH for den trees used by *P. ariel* was 41.7 cm, ranging from 18.3 to 77.0 cm, while mean DBH for den trees used by *M. gouldii* was 36 cm (range 12–63 cm; Griffiths et al. 2001) and 30.5 cm for *C. penicillatus* (range not specified; Firth et al. 2006). All three arboreal mammal species also favoured eucalypts as den trees. Thus, there is no evidence to suggest that *C. penicillatus* and *M. gouldii* require markedly larger or different species of den trees than *P. ariel*. Consequently, tree hollow availability alone unlikely explains why *P. ariel* has persisted in relatively low rainfall areas where other hollow-dwelling arboreal mammals have disappeared. However, the use of dens on the ground (such as fallen logs; Griffiths et al. 2001 and Firth et al. 2006) and the associated terrestrial behaviour of *C. penicillatus* and *M. gouldii* may have made these

Figure 5. Relationships between diameter at breast height (DBH) and: (A) maximum canopy diameter; and (B) tree height, sites based on terrestrial LiDAR-derived measures of tree structure. High rainfall (dark red) and low rainfall (dark blue) sites are shown separately.
species more exposed and vulnerable to ground-based predation, compared to *P. ariel* which is dependent on tree hollows and almost strictly arboreal due to its ability to glide between trees.

In areas of low rainfall, the canopy was more sparse and closer to the ground (indicated by lower values of canopy height, cover and tree density) than in areas of high rainfall. It is, therefore, plausible that non-gliding arboreal mammals may be more susceptible to ground-based predation in areas of low rainfall, simply because they are forced to forage and den closer to the ground (in shorter trees) and spend more time on the ground moving between trees. Unfortunately, there is currently no available research on the movement behaviour of such species to test this theory. However, both the common brushtail possum (*Trichosurus vulpecula*) and *C. penicillatus* have been found to maintain higher abundance in areas of greater shrub density, where there is presumably better cover from predators, including feral cats (Davies et al. 2017b; Stobo-Wilson et al. 2019). Variation in terrestrial behaviour among northern Australia’s arboreal mammals, as opposed to variation in den-tree requirements and hollow availability, more likely explains why some species have declined more severely than others.

Table 5. Relative variable importance (RVI) of measures of tree size and site on *Petaurus ariel* den-tree selection; calculated from Akaike weight’s using generalized linear models.

| Predictor variable | RVI |
|--------------------|-----|
| Log10 DBH          | 1.00|
| Site               | 0.99|
| Log10 DBH × Site   | 0.82|
| Canopy shape       | 0.55|
| Tree height        | 0.38|
| Canopy shape × Site| 0.37|
| Canopy perimeter/area | 0.37 |
| Maximum canopy distance | 0.34 |
| Tree height        | 0.34|
| Maximum canopy distance × Site | 0.12 |
| Canopy perimeter/area × Site | 0.12 |
| Tree height × Site | 0.11|

Variables with a RVI > 0.73 (bolded) are considered significant predictor variables and were included in the best model.

Table 6. Model selection results for negative binomial generalized linear models of number of visible tree hollows as a function of tree species, site and diameter at breast height (DBH). Data were derived from all trees that were physically measured at each site (this includes den trees). ΔAIC represents the difference between the model’s AIC (Akaike’s Information Criterion) value and that of the top-ranking model, wi is the Akaike weight. The grey highlighted model is the null hypothesis model and bold text indicates the most supported models (ΔAIC ≤ 2).

| Model                | ΔAIC | wi  | R²  |
|----------------------|------|-----|-----|
| Log10 DBH + Species  | 0.00 | 1.00| 0.47|
| Null                 | 15.86| 0.00| 0.49|
| Site                 | 147.16| 0.00| 0.00|
| Species              | 149.11| 0.00| <0.01|
| Site × Species       | 150.22| 0.00| 0.02|

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Conclusion

Significant variation in the habitat structure of high and low rainfall areas within the tropical savanna of northern Australia has a substantial influence on den-tree selection by the arboreal marsupial, P. ariel. However, at both sites P. ariel selected den trees that were more likely to be hollow bearing. We found TLS to be a useful tool for mapping fine-scale variation in habitat structure which enabled us to account for variation in den-tree selection between sites. The findings from this study, along with previous studies on arboreal mammal habitat use in northern Australia, highlight that hollow-bearing eucalypts are an essential resource for arboreal mammals in northern Australia’s tropical savannas. Therefore, to protect arboreal mammal populations land management practices in northern Australia should seek to protect hollow-bearing eucalypt trees. At a landscape scale this may be achieved through improved fire management (Woolley et al. 2018). Regardless, similarity of den trees used by P. ariel and other more severely declining arboreal mammals, suggests reduction in hollow availability cannot fully explain the disproportionate decline in arboreal mammals in northern Australia’s tropical savannas. Instead, the higher degree of arboreality of P. ariel may have (somewhat) reduced this species susceptibility to ground-based predation relative to other arboreal mammals.

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Supporting Information
Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table A1. Model selection results for generalized linear models assessing den selection by *Petaurus ariel*. ΔAIC represents the difference between the model’s AIC (Akaike’s Information Criterion) value and that of the top-ranking model; wi is the Akaike weight. The grey highlighted model is the null hypothesis model and bold text indicates the most supported models (ΔAIC ≤ 2).