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## Roost site selection by southern forest bat *Vespadelus regulus* and Gould's long-eared bat *Nyctophilus gouldi* in logged jarrah forests; south-western Australia

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### ABSTRACT

Information on roosting requirements and responses to forest management is integral to effectively conserve and manage bat populations. Tree hollows are especially important for roosting bats given the long time taken for hollows to form. We used radiotelemetry to compare roost site selection in two species, *Vespadelus regulus* and *Nyctophilus gouldi*, in logged jarrah forests of south-western Australia. We compared characteristics of roost trees and forest structure around roost trees ( $n = 48$ ) with randomly located plots at a local roost tree level ( $n = 90$ ) in February and March 2009. For landscape features, we compared roost trees with randomly selected trees in the broader landscape that had cavities or exfoliating bark ( $n = 204$ ). *V. regulus* roosted solely in hollows that were located predominantly in contemporarily unlogged buffers and mature forest while *N. gouldi* used a broader range of roost types, located in contemporarily unlogged buffers and mature forest and in retained habitat trees in gap release and shelterwood creation silvicultural treatments. In contrast with *N. gouldi*, which selected hollows or crevices under bark near the ground and close to vegetation, *V. regulus* used hollows that were high above ground and had little surrounding vegetation. Both species preferred large trees, in intermediate or advanced stages of decay and crown senescence. Bats changed roosts frequently, with short distances between subsequent roosts, suggesting a degree of spatial fidelity. Contemporarily unlogged buffers and mature forest contained higher densities of trees with hollows than gap release and shelterwood creation areas, potentially providing more alternate bat roosts. Our results demonstrate the importance of mature forest and unlogged buffers as bat roost sites in logged jarrah forests of south-western Australia, but the area of old forest required by these and co-occurring bat species remains to be determined.

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### 1. Introduction

The management of wildlife populations requires an understanding of how individuals use their habitat, and this knowledge is particularly important for the conservation of threatened or declining species. One group that appears to be in global decline are bats (Hutson et al., 2001) yet, for many bat species, very little is known about how they use their habitat or their sensitivity to habitat modification. This information is, however, critical if bats are to be successfully conserved and managed. One major threat facing bats worldwide is timber harvesting (Hutson et al., 2001) and the destruction and alteration of roost sites is thought to be one of

the main ways that timber harvesting impacts on bat populations. Therefore, in areas where timber harvesting occurs, it is critical that we understand the roosting requirements of bats if we want to effectively conserve and manage bat populations.

Conservation of roost sites is critical if bat populations are to be conserved and maintained because bats spend a large portion of their life in roosts and use them for a wide variety of important functions. These functions include as diurnal shelter, maternity, bachelor, migrating, and hibernation sites (Kunz and Lumsden, 2003). Roost sites can also facilitate complex social interactions, including information transfer, act as breeding sites for rearing young and mating (Kunz, 1982; Willis and Brigham, 2004), offer protection from inclement weather, minimize parasite load (Lewis, 1996), promote energy conservation and reduce predation risks (Rydell et al., 1996; Vonhof and Barclay, 1996; Turbill et al., 2003; Turbill and Geiser, 2005; Turbill, 2006). As only a few bat species are known to manipulate the physical structure of their roosts, the

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survival and reproductive success of bats is strongly influenced by the type and location of existing roosts present in an area (Racey and Swift, 1981; Brigham and Fenton, 1986; Vonhof and Gwilliam, 2007). Therefore, the maintenance of existing roost sites is important for the survival of bat populations.

Timber harvesting, as well as forest clearing and fragmentation, typically leads to a reduction in numbers of large live and standing dead trees (Laurance et al., 2000; Gibbons et al., 2008; Oliveira et al., 2008). In Australia, this situation is manifested in the loss of older trees, which may threaten the survival and persistence of bats and other vertebrate wildlife dependent on this resource (Lunney et al., 1988; Lindenmayer and Franklin, 2002; Lunney and Matthews, 2004). The importance of large, hollow-bearing trees as roosts for many bats is well documented in the literature (Taylor and Savva, 1988; Hosken, 1996; Law, 1996, 2004). More than 50% of Australia's insectivorous bats roost and breed in tree hollows (Tidemann and Flavel, 1987; Churchill, 2008) with large hollows being particularly important for maternity roosts (Law and Anderson, 2000; Lumsden et al., 2002a). Large, hollow-bearing trees also provide exfoliating bark and bark fissures, which are also important roost sites for some bat species, at least for part of the year (Goldingay, 2009). These species include *Nyctophilus bifax* (Lunney et al., 1995), *N. geoffroyi* (Taylor and Savva, 1988; Lumsden et al., 2002a), *Nyctophilus gouldi* (Lunney et al., 1988; Tidemann and Flavel, 1987) and *N. timoriensis* (Churchill, 2008), but, even in these species maternity roosts typically occur in tree hollows (e.g. Lunney et al., 1988; Lumsden et al., 2002a; Goldingay, 2009), highlighting the importance of tree hollows as key resources for bats.

Hollows may provide optimal microclimates for maternity roosts because they are better insulated against inclement weather than roosts under bark (Sedgeley, 2001; Lumsden et al., 2002a). Such hollows are more likely to occur and be used by bats in large trees that are many centuries old (e.g. Mackowski, 1984; Gibbons et al., 2000; Lindenmayer et al., 2002; Whitford, 2002; Smith et al., 2008) and the time required for hollows to develop, that are suitable for use by fauna, is generally much longer than the time between timber-harvesting events in production forests (e.g. Ball et al., 1999; Whitford, 2002; Whitford and Stoneman, 2004). The lag times thus make bats vulnerable, given the short logging rotations prevalent in Australia (Parnaby and Hamilton-Smith, 2004). Consequently, many bat species may be negatively impacted by the removal of large and older trees during logging, which leads to a reduction in the number of suitable roost sites and possibly render roost sites in remaining trees suboptimal (Goldingay, 2009).

Information on the dependence of birds and non-volant mammals on hollows in older trees in Australia is more extensive (e.g. Abbott and Whitford, 2002; Gibbons and Lindenmayer, 2002) than our knowledge of bat requirements. Various management prescriptions in production forests are intended to mitigate impacts on hollow-roosting species, including retention of old-growth habitat, riparian buffers and other unlogged reserves (see Lindenmayer and Franklin, 2003) and the retention of hollow-bearing trees within logged forests (CCWA, 2003). Riparian zones have been shown to provide foraging and drinking habitat (Law and Chidel, 2002; Lloyd et al., 2006), as well as roosting habitat, for many bats (Lunney et al., 1988; Taylor and Savva, 1988; Law and Anderson, 2000; Schulz, 2000), however, it remains to be determined whether bats use either the retained unlogged habitat or the retained hollow-bearing trees after logging. Furthermore, whether unlogged habitat patches are sufficiently large to allow for temporal changes in roost requirements, or how much unlogged habitat is enough for the long-term persistence of bats remains to be determined (Law, 1996).

Whereas a number of studies have investigated roosting requirements of bats, especially in eastern Australia (e.g. Taylor and Savva, 1988; Lunney et al., 1988, 1995; Law and Anderson, 2000; Lumsden et al., 2002a), there is a general dearth of information

regarding impacts of roost-site reductions on the survival of a wide range of bat species in other areas of Australia, including Western Australia. Furthermore, temporal and spatial changes in the use of hollows and crevices under exfoliating bark by particular species have not been examined. Yet, to verify effective management, there needs to be a sound knowledge of both the specific requirements of each bat species and the availability of roost types (bark, hollows, etc., Goldingay, 2009). While bats make up a significant proportion of the mammal fauna in the jarrah forest of south-western Australia (9 of around 30 native extant species), little is known about their roosting requirements or their responses to the removal of suitable roost sites, and it is unclear whether we can extrapolate results from eastern Australia. We investigated the sensitivity of two sympatric species of jarrah forest-dwelling vespertilionid bats, the southern forest bat *Vespadelus regulus* and Gould's long-eared bat *N. gouldi*, to the loss of roost sites from recently logged forests and the effectiveness of current management practices at conserving appropriate roost sites. The two species were selected because they have small home ranges and were, therefore, logistically easier to track to their day roosts. Furthermore, these species display different wing morphologies and echolocation call attributes, both potentially influencing how each species uses a logged landscape. Although some studies describe the roost requirements of *N. gouldi* elsewhere (Lunney et al., 1988; Turbill, 2006), little is known about the roosting requirements of *V. regulus*, although Taylor and Savva (1988) tracked two female *V. regulus* bats to four roost hollows in live and dead Eucalypt trees in Tasmania.

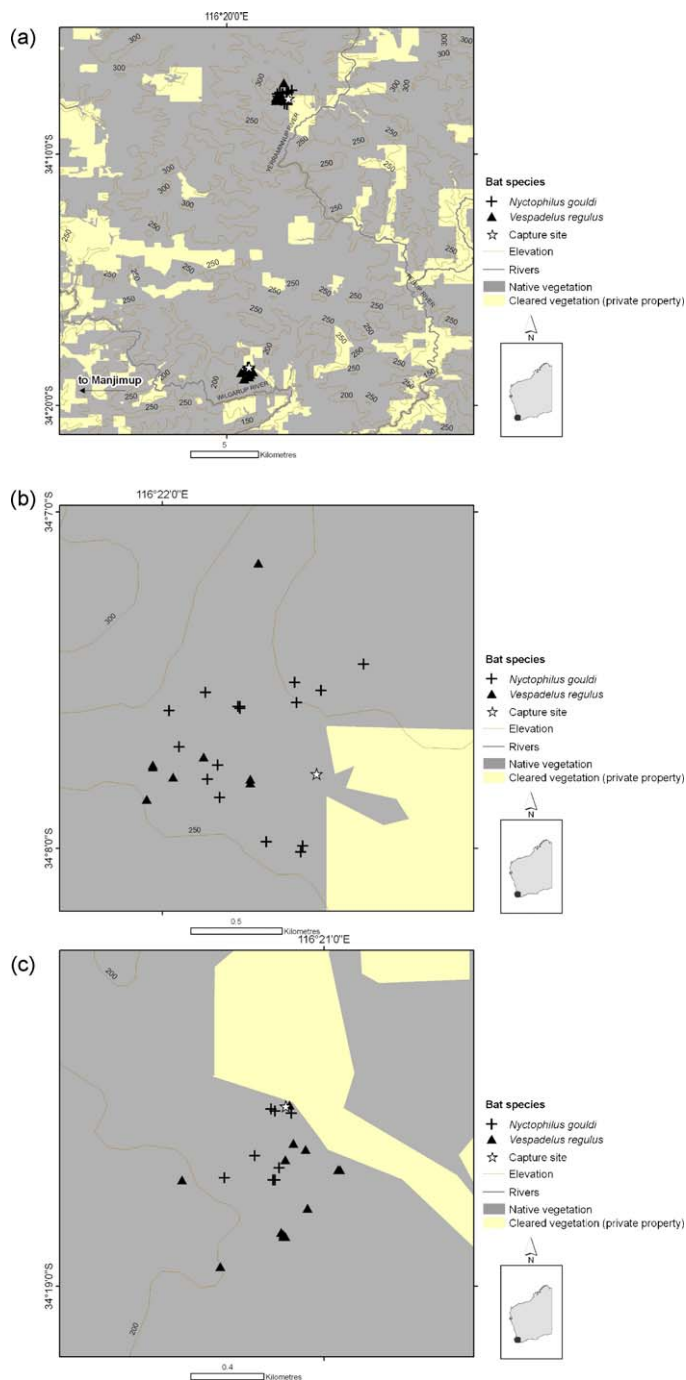
To better understand the roosting-habitat requirements of the two species as influenced by logging, we studied inter-specific patterns of roost site selection. Based on previous studies on the same or congeneric species (e.g. Lunney et al., 1988; Herr and Klomp, 1999; Law and Anderson, 2000; Campbell et al., 2005), we predicted that roost trees of the two species would be larger and less cluttered by surrounding vegetation than random trees. Our study objectives were to (1) investigate roost and site selection by bats in logged forests by comparing roost trees (and the surrounding habitat) with potential roost trees and surrounding plots to identify important roost habitat characteristics; (2) compare roost and site characteristics of *N. gouldi* with those of *V. regulus*; and (3) determine the relative importance of buffer zones and other unlogged areas as roosting habitat for bats in logged jarrah forests, south-western Australia.

## 2. Material and methods

### 2.1. Study area

The study was conducted east of Manjimup and Bridgetown in the southern jarrah forest of Western Australia (Fig. 1a, b and c). The area has a Mediterranean-type climate with cool, wet winters and warm summers (Gentilli, 1989). Monthly average minimum and maximum temperatures respectively vary from 5.7 to 12.9°C and 15.5 to 27.6°C. Annual average rainfall at Manjimup and Bridgetown is 1011.8 and 829.4 mm respectively, with over 70% falling between May and September at both locations.

The study area was primarily jarrah forest interspersed with some patches of farmland. Jarrah forest is a dry sclerophyll forest type where jarrah (*Eucalyptus marginata* Donn. ex. Smith, 1802) is the dominant tree with marri (*Corymbia calophylla* K.D. Hill and L.A.S. Johnson) also common in many areas. Understorey species richness is generally high (Havel, 1975a,b; Commonwealth of Australia and Western Australian Government, 1998). Typical mid-story species include jarrah, marri and bull banksia (*Banksia grandis*). Common understorey plants include *Acacia pulchella*, *Bossiaea ornata*, *B. linophylla*, *Hakea lissocarpha*, *Leucopogon capitell-*



**Fig. 1.** General map showing bat roost and capture sites. Inset shows the location of the study area within Western Australia. b. Map showing bat roost sites at the northern capture site of the study area. Inset shows the location of the study area within Western Australia. c. Map showing bat roost sites at the southern capture site of the study area. Inset shows the location of the study area within Western Australia.

*latus*, *L. verticillatus*, *L. propinquus*, *Lomandra* sp., *Macrozamia riedlei*, *Myoporum* sp., *Persoonia longifolia*, *Xanthorrhoea gracilis* and *X. preissii*.

## 2.2. Logging history

A description of the history of logging in the jarrah forest is given by Abbott and Loneragan (1986), Stoneman et al. (1989) and Bradshaw (1999), including how logging practices have changed

over time. The current methods have been in place since 1985 and include: (1) 'Gap Release', involving the removal of about 95% of mature overstorey to provide opportunity for a regenerating tree cohort, with four to five habitat trees (those with characteristics that give them a high probability of containing hollows suitable for fauna) and six–eight potential habitat trees retained per hectare; and (2) 'Shelterwood Creation' involving the retention of 40–60% of basal area after logging to provide seed for regeneration. Gaps are  $\leq 10$  ha in size, variable in shape and do not extend across ridges while shelterwoods have no size limitation and can extend across ridgelines. Buffers of unlogged forest between gap release patches and along riparian areas, including streams and creeks, are also designated within logged areas. Other areas excluded from logging include diverse ecotype zones, road reserves, uneconomic areas, old-growth forest, native forest retained for research purposes, and fauna habitat zones.

Much of the study area (Kingston and Warrup Forest blocks) has experienced at least one cycle of timber harvesting since about 1920. Only about 6% is recorded as not having been logged. About 20% of the total area has been logged since 1980 constituting at least the second time these particular stands have been harvested: generically referred to here as 'regrowth' forest. The remainder of the area (74%) was last harvested prior to 1980, when logging operations characteristically removed very small timber volumes and were variable both spatially and temporally (Bradshaw, 1999). Referred to here as 'mature' forest, these areas tended to be very selectively harvested, thereby retaining many of the characteristics of a mature stand including a relatively greater abundance of large trees and a relatively more open understory and mid-story compared with more recently logged areas.

## 2.3. Field methods

Bats were initially captured in February and March 2009 using harp traps (Two-Bank 4.2 square metres; Austbat Research Equipment, Victoria) at two different water holes within different logging histories (Fig. 1a, b and c). Data collected from each captured bat included species, age (juvenile, subadults, adults), sex, mass (to nearest 0.2 g using Pesola spring scales), and reproductive condition. We determined female reproductive condition by palpating the abdomen and inspecting the mammae and determined age-class by examining the degree of epiphyseal–diaphyseal fusion (Racey, 1988). Individual bats of both species were radio-tracked by attaching miniature position-sensitive single-stage radio transmitters with 18–20 cm antenna attached to the dorsal fur using Superglue. Transmitters weighing 0.40–0.43 g (Titely Electronics, Ballina) were fitted to *N. gouldi* bats and others weighing 0.36–0.40 g (Holohil Systems Ltd., Woodlawn, Ontario, Canada) were fitted to *V. regulus* bats.

For *N. gouldi*, transmitters weighed less than the 5% body mass guideline in which transmitter weight can influence flight performance (Aldridge and Brigham, 1988). However, for *V. regulus*, transmitters weighed 5–8% of body mass. Other studies have successfully radio-tracked microbats with transmitters representing at least 8% of body mass (e.g. Lunney et al., 1995; Law and Anderson, 2000; Lumsden et al., 2002b; Campbell et al., 2005).

Bats were monitored using Australis 26k Scanning Receivers and AY/C Yagi 3 element collapsible hand-held antennas. We tracked individual bats to their day roosts on consecutive days until transmitters dropped off or the battery failed (ca. 12 days;  $n=23$ ). Attempts were made to observe roost entrances at dusk to determine the exact type and location of the roost in the tree and the colony size. To estimate local roost availability, a 0.03 ha circular plot (10-m radius) was marked and centred on the roost tree (Vonhof and Barclay, 1996). The species of the roost tree, logging history and the geographical location (using GPS) of the site were



**Table 1**

Variables measured for the roost sites of the southern forest bat (*Vespardelus regulus*) and Gould's long-eared bat (*Nyctophilus gouldi*) and comparative random sites in the jarrah forests, south-western Australia. Random trees were measured both locally around roost trees and in the broader forest landscape.

Variable	Category/Measurement (units)
Roost variables	Identification from leaf/bark characteristics
Diameter at breast height (DBHOB)	Using measuring tape at 1.3 m over bark
Height (m)	Measured using Tree Vertex
Height relative to canopy height (m)	Difference in roost tree and the canopy height. Canopy height measured as below
Snag class (decay stage)	1 = all live tree; 2 = <30% dead; 3 = >30% dead; 4 = 100% dead (Maser et al., 1979; Campbell et al., 2005)
Percent bark cover (bark-cover class)	1 = none; 2 = <10%; 3 = 10–25%; 4 = >25%
Crown senescence classification	Assessment of crowns as better (SENES 0) or worse (SENES 9 and 10) (Whitford, 2002)
Dead Branch Order (DBO)	Scale of assessing DBO (DB1–DB9). DB9 is a tree trunk more deteriorated than DB8 (Whitford, 2002)
Location	Recorded using GPS
Distance from previous roost, if any (m)	Straight-line distance generated from differential GPS
Distance from capture site	Straight-line distance generated from differential GPS
Roost variables	
Roost type <sup>a</sup>	Hollow, under bark, fissure, other
Roost entrance height <sup>d</sup>	Identified the cavity/bark occupied by assessing radio-signal strength and direction when standing near the tree. Measured height using Tree Vertex
Site variables (extrinsic variables)	
Distance to nearest five available trees (m)	Measured using Laser Rangefinder for trees $\geq 20$ cm DBHOB in 0.03-ha plot
Height of available nearest tree (m)	Measured using Tree Vertex for nearest tree $\geq 20$ cm DBHOB in 0.03-ha plot
Mean canopy height (m)	Four randomly selected trees within plot or extra trees measured as required using Tree Vertex
Mean canopy cover	Four densiometer readings, 90° apart, at each plot, 25 m from the roost tree
Vegetation clutter indices <sup>b</sup>	Foliage cover scores for the upper stratum ( $\geq 15$ m), mid-storey stratum (5–15 m), woody-seedling (shrubs) stratum (0.75 cm–5 m) and herbaceous groundlayer stratum (0–0.75 cm): 1 = very sparse (0–5%); 2 = sparse (5–25%); 3 = moderate (26–50%); 4 = mid dense (51–75%); 5 = dense ( $\geq 75\%$ )
Slope (degree)	Obtained from GIS data of the study area
Elevation (m)	From GIS data of the area
Distance to nearest water point	Distances obtained from GIS data of the study area
Distance to nearest creek line or watercourse	From GIS data
Distance to nearest gap or shelterwood	From GIS data

<sup>a</sup> Only measured for roost trees.

<sup>b</sup> Each stratum score was weighted (multiplied) by its height to get the final clutter index for that stratum (Law and Chidel, 2002).

recorded. A variety of roost tree and site characteristics were then measured (Table 1).

To estimate roost availability in the surrounding forest landscape, a sample of random trees were measured for comparison with roost trees and an additional plot established around these randomly selected trees. At the local roost tree scale, this plot was located by selecting a random point between 100 and 300 m from the roost tree in a randomly selected direction (Vonhof and Gwilliam, 2007). From the random point, one random tree was selected from a sample of four trees from the four compass directions, and a plot was marked around this random, focal tree. Only trees with DBHOB  $\geq 20$  cm and with at least one observable hollow or peeling bark were selected. The tree and site characteristics of the focal tree were measured as for roost trees. For comparison of landscape features of roost trees with random trees at the landscape scale, mature trees (DBHOB  $\geq 80$  cm; Lunney et al., 1988) with at least one observable hollow and/or peeling bark were selected randomly in 10 50 × 50 m plots in each of the following logging histories; gap release, shelterwood creation, gap buffers, riparian buffers and mature forest. These plots were also used to estimate the density of trees with hollows and/or peeling bark in the landscape.

#### 2.4. Statistical analyses

All variables were continuous or rank ordered (Table 1). Data from five *N. gouldi* roosts (blackbutt *Eucalyptus patens*;  $n = 3$  and balga *Xanthorrhoea preissii*;  $n = 2$ ) were not considered in the analysis of roost characteristics because of small sample sizes. We analyzed data for marri and jarrah roost trees separately, to account for the structural differences between the two tree species, since these were predominantly selected as roost sites.

Tree, roost and site variables were initially compared using Spearman rank correlations. Where pairs of variables had correlation coefficients greater than 0.8, one of the pair was excluded from further analysis. For instance, to test for differences in clutter levels between roost and random plots, we first determined relationships between clutter indices for each stratum. Ground, shrub and mid-storey indices were highly correlated with each other ( $0.81 < r < 0.84$ ,  $P < 0.001$ ), but none were correlated with canopy clutter, thus, in analyses, the three sub-canopy indices were summed together, resulting in only two, the sub-canopy and the canopy indices (Table 1).

Roost trees used by each species (*V. regulus* and *N. gouldi*) were compared to random trees to test whether they were distinct from the local and landscape population of available trees. Direct interspecific comparisons of the characteristics of roost trees were made to investigate species-specific preferences for roost tree and site characteristics. We used the Bray–Curtis association measure to assess similarities among roost and random trees with respect to variables related to tree and site characteristics (Table 1). Semi-strong hybrid multidimensional scaling ordination was used to explore relationships and to provide, in a few dimensions, an accurate representation of the similarity between roost and available trees on the basis of their attribute profiles (tree/site characteristics) (Rhodes and Wardell-Johnson, 2006). An Analysis of Similarity (ANOSIM) was then applied to test for the significance of any differences. Mann–Whitney U-tests were used to compare means and frequencies of use and availability for roost trees and random trees and site characteristics for both continuous and ordinal variables because data were heteroscedastic. A Student's *t*-test was used to test for differences in the distance moved between capture sites and roost trees and between successive roosts, with species as a factor and distances as dependent variables. To compare continu-

ous variables of roost trees used by *V. regulus* with those used by *N. gouldi* after transforming the data using  $\log_e(x+1)$ , two-sampled *t*-tests were used with species as a factor. Differences between logging histories (gaps, shelterwoods, gap buffers, riparian buffers and mature forest) in the density of trees with hollows were tested using one-way ANOVA with logging history and density as the predictor and dependent variables, respectively. *Post-hoc* Tukey tests were performed to check for significant differences between treatments (Day and Quinn, 1989). Significant results are presented at the level of  $P=0.05$ . All means are presented  $\pm$ SE. These analyses were carried out using Statistica 7.0 (Statsoft, Inc., Oklahoma, USA).

### 3. Results

#### 3.1. Radio-tracking

We attached transmitters to 12 *V. regulus* and 11 *N. gouldi* (Table 2), of which 64% of *N. gouldi* and 83% of *V. regulus* were females, all nonparous at the time of transmitter attachment. Two transmitters attached to *V. regulus* either failed, or bats could not be located after the first night, while the remaining 10 bats were tracked to 21 different roost trees for a mean of  $5.9 \pm 1.6$  days. For *N. gouldi*, all 11 bats were tracked to 27 different roost trees for a mean of  $4.3 \pm 0.9$  days (Table 2). The roosts for both bat species occurred primarily in two species of trees, jarrah ( $n=32$ ) and marri ( $n=11$ ). *N. gouldi* also used blackbutt ( $n=3$ ) and balga ( $n=2$ ) as roosts.

*N. gouldi* roosts were closer ( $340.2 \pm 59.7$  m;  $n=11$ ) to capture sites, compared to *V. regulus* ( $465.5 \pm 89.8$  m;  $n=10$ ) ( $t_{19} = -2.23$ ;  $P=0.038$ ) (Fig. 1a, b and c). Bats changed roosts every  $2.8 \pm 0.3$  ( $n=11$ ) and  $2.3 \pm 0.5$  ( $n=10$ ) days for *N. gouldi* and *V. regulus*, respectively. We documented eight cases where individual bats vacated a roost tree for between 2 and 4 days and then returned to that roost tree while still carrying a transmitter (*N. gouldi*,  $n=1$ ; *V. regulus*,  $n=7$ ). *N. gouldi* moved  $164 \pm 16$  m ( $n=16$ ) between consecutive roosts while *V. regulus* moved  $400 \pm 38$  m ( $n=13$ ) and this difference was significant ( $t_{27} = -5.48$ ;  $P < 0.001$ ).

It was not possible to determine the sex and age structure of bat species within roosts as attempts to trap at one *V. regulus* communal roost failed. However, based on emergence counts ( $n=9$ ) at this communal roost, the colony ranged from 10 to 15 individuals over 9 days, with a mean colony size of  $12.3 \pm 0.5$  bats. The sex composition of the communal roost could not be determined either, except for the two females with transmitters. In addition, on separate occasions, and in separate balga roosts, 25 and 18 *N. gouldi* bats were counted as they exited after their roosts were disrupted.

#### 3.2. Comparisons of roosting characteristics of *V. regulus* and *N. gouldi*

*V. regulus* selected roosts exclusively in hollows formed in trunks or branches of either dead standing trees (snags; 72%) or live marri and jarrah trees (28%). In contrast, *N. gouldi* showed a high versatility in the choice of roosts, roosting in spaces under exfoliating bark in both dead and live trees (44%), hollows (33%), cracks (15%) and even under balga skirts (7%). One female *N. gouldi* roosted in a hollow of a burnt-out jarrah log (length = 7.48 m; diameter = 56 cm) on the ground for two consecutive days.

Both *V. regulus* and *N. gouldi* roosted in trees with a larger diameter ( $>80$  cm DBHOB) than random trees (Tables 3 and 4), but DBHOBs of both marri and jarrah trees used for roosting did not differ between bat species (Table 5). *V. regulus* selected taller jarrah trees for roosting than *N. gouldi* (Table 5), but there was no significant difference in mean height for marri roost trees between the two species. Even so, since a significant proportion of *V. regulus* roosts ( $n=18$ ) were in jarrah trees with only three roosts located in

marri trees, it can be presumed that, in general, *V. regulus* selected significantly taller trees than *N. gouldi* (Table 5). Furthermore, the mean canopy height of roosting plots used by *V. regulus* was significantly greater than those used by *N. gouldi*, although the sites had similar canopy cover for both bat species (Table 5).

The two bat species also exhibited differences in roost heights. Even after excluding log and balga roosts, roost entrance heights of *N. gouldi* were significantly lower than those of *V. regulus* for both jarrah and marri tree roosts. Roost entrances of *N. gouldi* tended to be situated below the level of the canopy while those of *V. regulus* were within the canopy (Table 5).

#### 3.3. Roost characteristics

Based on tree and site variables, roost trees selected by both *V. regulus* and *N. gouldi* grouped separately from random trees in the MDS (Fig. 2). Marri and jarrah roosts used by *V. regulus* were greater in DBHOB and height compared to random trees (Table 3), and they were as tall as, or taller, than the forest canopy ( $t_{41} = -0.26$ ;  $P=0.799$ ). Furthermore, distances to the five nearest available trees were significantly greater for jarrah roosts than for random trees (Table 3). However, marri roosts of *V. regulus* showed non-significant results for these variables, although the sample size was very small ( $n=3$ ). There were no significant differences in mean canopy height and mean canopy cover between roost plots of *V. regulus* and random plots for either tree species (Table 3).

Unlike *V. regulus*, roosting trees selected by *N. gouldi* had similar height to random trees (Table 4) but, relative to the overall canopy height, the roost trees were, on average, significantly shorter ( $t_{42} = -2.03$ ;  $P=0.048$ ) (Table 4). This indicates that *N. gouldi* selected roosts within the sub-canopy. However, the mean DBHOB of both jarrah and marri trees used as roosts by *N. gouldi* were significantly greater than random trees (Table 4). The mean height of the nearest available trees was significantly less for jarrah roost trees than random trees, although marri roost trees did not show any differences. This was also true for mean canopy cover with jarrah roosts located in plots showing significantly less canopy cover than random locations, but no difference between marri roost plots and random locations (Table 4). Neither distances to the five nearest available trees nor mean canopy heights differed significantly between roost and random locations for either tree species (Table 4).

Both bat species displayed a clear preference for roosting in trees that contained  $>30\%$  dead wood (Decay Stages 3 and 4; Table 1) while random trees, in comparison were all alive or  $<30\%$  dead (Decay Stages 1 and 2, Table 1). Roost trees were also, on average, at a more advanced stage of crown senescence, from moderate to advanced states of deterioration (Dead Branch Order; Table 1), compared with random trees (Tables 3 and 4). In addition, bats selected roosting trees with a bark cover of less than 25% (Bark Cover Classes 1, 2 and 3; Table 1), compared with random trees which had a bark cover of more than 25% (Bark Cover Class 4; Tables 3 and 4).

#### 3.4. Selection of roosts and landscape features

Most roosts of *V. regulus* were in mature forest ( $n=15$ ; 71.4%), with the remainder in riparian buffers near ephemeral creek lines ( $n=5$ ; 23.8%) and a marked retained habitat tree in a shelterwood creation treatment ( $n=1$ ; 4.8%). No *V. regulus* roosts were observed in young regrowth forest. As 95% of *V. regulus* roosts were in "mature forest", including riparian buffers, there was a significant preference for this forest type ( $\chi^2=6.50$ ,  $P < 0.011$ ), given that "mature forest" comprises approximately 80% of the study area (P. Collins, DEC, pers. comm.). By contrast, *N. gouldi* showed greater versatility in the location of roosts, selecting roosts in riparian buffers ( $n=8$ ; 29.6%), mature forest ( $n=8$ ; 29.6%) and remnant

**Table 2**

Number of transmitters attached to each sex and species of bat, the number never located, number of roosts located and the corresponding number of potential roost trees measured in the jarrah forests, south-west Western Australia. The number of individuals found in one roost is the difference between column 3 and the sum of columns 7, 8 and 9.

Species	Sex	No. of transmitters fitted	No. never located	Total No. of roosts located	Total No. of available trees measured	No. of individuals found in two roosts	No. of individuals found in three roosts	No. of individuals found in ≥ 4 roosts
<i>N. gouldi</i>	F	7	0	19	34	2	3	1
	M	4	0	8	18	2	1	0
Subtotal		11	0	27	52	4	4	1
<i>V. regulus</i>	F	10	1	19	36	4	0	2
	M	2	1	2	2	1	0	0
Subtotal		12	2	21	38	5	0	2
Total		23	2	48	90	9	4	3

trees in shelterwoods ( $n = 10$ ; 37.0%) as well as one large diameter tree in the gap release ( $n = 1$ ; 3.7%). Based on the areal extent of these forest types, this species selectively roosted in shelterwood and gap forests that have been logged since 1985 ( $\chi^2 = 28.65$ ,  $P < 0.001$ ). The density of large diameter trees (DBHOB > 80 cm) with hollows and/or peeling bark differed significantly between forest treatments ( $F_{4,45} = 61.00$ ,  $P < 0.001$ ). Riparian buffers had the highest density ( $21.6 \pm 18.6$  trees  $ha^{-1}$ ), followed by mature forest ( $21.2 \pm 18.3$  trees  $ha^{-1}$ ) and gap buffers ( $18.4 \pm 15.8$  trees  $ha^{-1}$ ), and there was no difference between these three treatments, but each had greater densities than either gap release ( $5.6 \pm 4.9$  trees  $ha^{-1}$ ) or shelterwood creation silvicultural treatments ( $9.2 \pm 7.9$  trees  $ha^{-1}$ ) ( $P < 0.05$ ).

For *N. gouldi*, roost sites in both jarrah and marri were closer to the nearest water points than random plots (Table 4). In contrast, *V. regulus* did not show any preferences for roosting closer to water points, but its roosts were at lower elevations than random locations (Table 3).

**Table 3**

A comparison of continuous and ordinal variables for roost trees and plots of southern forest bats (*Vespadelus regulus*) roosts with random trees and plots in the jarrah forests, south-western Australia, February–March 2009. Means ( $\pm$ S.E.) are presented, as are Mann–Whitney U-test results with associated probabilities. Significant results at  $P = 0.05$  are shown in bold.

Variable	Jarrah		Marri		Mann–Whitney U-tests			
	Roost ( $n = 18$ )	Random ( $n = 25$ )	Roost ( $n = 3$ )	Random ( $n = 12$ )	Jarrah		Marri	
					$Z_{Adj}$	$P$	$Z_{Adj}$	$P$
Tree characteristics								
DBHOB (cm)	89.5 $\pm$ 7.4	41.1 $\pm$ 2.8	88.6 $\pm$ 21.2	33.5 $\pm$ 2.3	4.79	<b>&lt;0.001</b>	2.62	<b>0.008</b>
Tree height (m)	33.3 $\pm$ 1.3	27.3 $\pm$ 1.4	32.4 $\pm$ 3.3	23.1 $\pm$ 1.1	2.62	<b>0.009</b>	2.31	<b>0.021</b>
Height relative to canopy height (%)	100.3 $\pm$ 3.9	85.0 $\pm$ 3.5	99.3 $\pm$ 5.4	79.3 $\pm$ 7.5	2.63	<b>0.008</b>	2.02	<b>0.043</b>
Decay stage <sup>a</sup>	2.7 $\pm$ 0.2	1.4 $\pm$ 0.2	3.7 $\pm$ 0.3	1.3 $\pm$ 0.1	4.57	<b>&lt;0.001</b>	2.95	<b>0.003</b>
Bark-cover class <sup>a</sup>	3.7 $\pm$ 0.1	4.0 $\pm$ 0.0	3.0 $\pm$ 1.0	4.0 $\pm$ 0.0	-2.19	<b>0.028</b>	-2.00	<b>0.046</b>
Crown senescence classification <sup>a</sup>	6.0 $\pm$ 0.5	2.8 $\pm$ 0.4	8.0 $\pm$ 1.5	2.0 $\pm$ 0.3	4.14	<b>&lt;0.001</b>	2.60	<b>0.009</b>
Dead Branch Order (DBO) <sup>a</sup>	4.2 $\pm$ 0.3	2.7 $\pm$ 0.2	4.7 $\pm$ 0.3	2.1 $\pm$ 0.3	3.31	<b>&lt;0.001</b>	2.60	<b>0.009</b>
Site characteristics (extrinsic variables)								
Distance to nearest five available trees (m)	5.5 $\pm$ 0.3	4.1 $\pm$ 0.3	4.9 $\pm$ 1.3	5.0 $\pm$ 0.6	3.37	<b>&lt;0.001</b>	-0.58	0.564
Height of available nearest tree (m)	20.0 $\pm$ 1.4	25.1 $\pm$ 1.6	15.4 $\pm$ 3.0	21.5 $\pm$ 2.2	-2.19	<b>0.028</b>	-1.30	0.194
Mean canopy height (m)	33.3 $\pm$ 0.7	32.0 $\pm$ 0.5	32.5 $\pm$ 1.6	30.4 $\pm$ 1.5	1.95	0.052	0.58	0.563
Mean canopy cover	65.9 $\pm$ 2.1	68.2 $\pm$ 1.2	68.4 $\pm$ 8.3	67.3 $\pm$ 2.3	-0.15	0.883	0.00	1.000
Sub-canopy index	23.7 $\pm$ 1.9	42.0 $\pm$ 2.2	13.3 $\pm$ 2.7	32.4 $\pm$ 3.2	4.63	<b>&lt;0.001</b>	2.46	<b>0.014</b>
Canopy index	30.8 $\pm$ 2.7	43.2 $\pm$ 1.6	30.0 $\pm$ 8.7	53.8 $\pm$ 5.0	3.51	<b>&lt;0.001</b>	2.04	<b>0.041</b>
Landscape features <sup>b</sup>								
Slope (degree)	2.7 $\pm$ 0.4	2.7 $\pm$ 0.1	1.0 $\pm$ 0.0	1.4 $\pm$ 0.1	0.12	0.906	-1.48	0.139
Elevation (m)	207.0 $\pm$ 5.7	230.7 $\pm$ 3.1	199.7 $\pm$ 19.5	245.9 $\pm$ 4.2	-2.97	<b>0.003</b>	-2.05	<b>0.04</b>
Distance to nearest water point (m)	701.4 $\pm$ 48.5	704.4 $\pm$ 24.5	416.0 $\pm$ 225.7	537.7 $\pm$ 34.0	0.30	0.763	-0.57	0.570
Distance to perennial watercourses (m)	2100.7 $\pm$ 137.5	2382.9 $\pm$ 122.1	2152.6 $\pm$ 318.2	1476.1 $\pm$ 53.4	0.24	0.812	1.84	0.066
Distance to non-perennial watercourses (m)	248.5 $\pm$ 26.4	267.6 $\pm$ 13.7	173.8 $\pm$ 160.5	205.9 $\pm$ 13.3	-0.04	0.969	-0.73	0.467
Distance to nearest dams (m)	1960.4 $\pm$ 228.0	1980.5 $\pm$ 151.7	2350.4 $\pm$ 599.7	1915.6 $\pm$ 116.1	1.03	0.301	0.68	0.495
Distance to cleared land > 10 ha (m)	486.8 $\pm$ 66.3	484.2 $\pm$ 31.6	360.9 $\pm$ 206.2	377.4 $\pm$ 22.2	0.52	0.603	-0.18	0.856
Distance to nearest gap or shelterwood	197.0 $\pm$ 35.8	180.8 $\pm$ 21.4	212.2 $\pm$ 42.7	210.2 $\pm$ 22.6	-0.18	0.780	0.43	0.665

<sup>a</sup> Ordinal variables, all others are continuous.

<sup>b</sup> Random jarrah trees ( $n = 118$ ); random marri trees ( $n = 86$ ). Roost trees are the same as at the local scale.

There were only three inter-specific differences out of the eight landscape variables measured (Tables 1 and 5). *N. gouldi* roost sites in both jarrah and marri were significantly closer to water points than those of *V. regulus* (Table 5). For both tree species, *N. gouldi* also selected roosts closer to dams than *V. regulus* (Table 5). Lastly, *N. gouldi* roosts in marri were significantly closer to non-perennial watercourses than corresponding roosts of *V. regulus*.

#### 4. Discussion

##### 4.1. Roost and site selection

This is the first study to report on roost-site selection of bats in logged jarrah forests of south-western Australia. The data presented are, however, from a small number of observations on a small number of bats during late summer and autumn, outside the maternity season. For instance, bats were captured at only two water holes (Fig. 1b and c) and, therefore, it is possible that our

**Table 4**  
A comparison of continuous and ordinal variables for roost trees and plots of Gould's long-eared bat (*Nyctophilus gouldi*) roosts with random trees and plots in the jarrah forests, south-western Australia, February–March 2009. Means ( $\pm$ S.E.) are presented; as are Mann–Whitney U-test results with associated probabilities. Significant results at  $P=0.05$  are shown in bold.

Variable	Jarrah		Marri		Mann–Whitney U-tests			
	Roost (n = 14)	Random (n = 30)	Roost (n = 8)	Random (n = 21)	Jarrah		Marri	
					Z <sub>Adj</sub>	P	Z <sub>Adj</sub>	P
Tree characteristics (intrinsic variables)								
DBHOB (cm)	78.0 $\pm$ 7.4	34.8 $\pm$ 2.8	63.3 $\pm$ 8.9	40.1 $\pm$ 3.9	4.40	<b>&lt;0.001</b>	2.36	<b>0.020</b>
Tree height (m)	24.9 $\pm$ 3.2	26.3 $\pm$ 1.2	26.4 $\pm$ 3.5	26.0 $\pm$ 1.5	0.48	0.632	0.76	0.449
Height relative to canopy height (%)	81.5 $\pm$ 10.5	88.6 $\pm$ 4.3	85.6 $\pm$ 9.9	92.0 $\pm$ 4.3	0.15	0.880	-0.54	0.591
Decay stage <sup>a</sup>	3.2 $\pm$ 0.2	1.4 $\pm$ 0.1	3.3 $\pm$ 0.4	1.6 $\pm$ 0.1	4.82	<b>&lt;0.001</b>	3.11	<b>0.002</b>
Bark-cover class <sup>a</sup>	3.0 $\pm$ 0.2	4.0 $\pm$ 0.0	3.4 $\pm$ 0.3	4.0 $\pm$ 0.0	-4.81	<b>&lt;0.001</b>	-3.42	<b>&lt;0.001</b>
Crown senescence classification <sup>a</sup>	6.8 $\pm$ 0.8	2.2 $\pm$ 0.2	6.3 $\pm$ 1.2	2.1 $\pm$ 0.3	4.47	<b>&lt;0.001</b>	3.15	<b>0.002</b>
Dead Branch Order (DBO) <sup>a</sup>	4.6 $\pm$ 0.6	2.4 $\pm$ 0.2	5.0 $\pm$ 0.8	2.2 $\pm$ 0.2	3.19	<b>&lt;0.001</b>	3.01	<b>0.003</b>
Site characteristics (extrinsic variables)								
Distance to nearest five available trees (m)	5.4 $\pm$ 0.5	4.7 $\pm$ 0.3	5.2 $\pm$ 0.7	4.4 $\pm$ 0.5	1.18	0.236	1.02	0.305
Height of available nearest tree (m)	23.2 $\pm$ 1.9	27.5 $\pm$ 1.6	24.4 $\pm$ 3.2	25.3 $\pm$ 1.6	-2.28	<b>0.023</b>	-0.15	0.884
Mean canopy height (m)	30.6 $\pm$ 0.7	30.0 $\pm$ 0.7	30.3 $\pm$ 1.8	28.3 $\pm$ 1.0	0.43	0.668	1.20	0.232
Mean canopy cover	60.8 $\pm$ 2.7	67.5 $\pm$ 1.3	64.8 $\pm$ 5.5	66.2 $\pm$ 2.1	-2.18	<b>0.029</b>	0.05	0.961
Sub-canopy index	33.4 $\pm$ 3.2	34.3 $\pm$ 1.7	31.0 $\pm$ 4.2	35.9 $\pm$ 1.9	-0.06	0.949	0.69	0.491
Canopy index	40.7 $\pm$ 2.9	46.0 $\pm$ 1.6	46.9 $\pm$ 1.9	43.6 $\pm$ 1.8	1.53	0.126	-1.06	0.282
Landscape features <sup>b</sup>								
Slope (%)	3.36 $\pm$ 0.5	2.96 $\pm$ 0.1	4.0 $\pm$ 0.7	2.9 $\pm$ 0.2	0.84	0.402	1.70	0.090
Elevation (m)	221.1 $\pm$ 8.3	231.6 $\pm$ 3.2	241.8 $\pm$ 5.5	242.4 $\pm$ 4.4	-1.02	0.308	0.05	0.962
Distance to nearest water point (m)	492.3 $\pm$ 21.0	774.7 $\pm$ 32.6	608.4 $\pm$ 49.5	773.8 $\pm$ 32.3	-2.76	<b>0.006</b>	-2.41	<b>0.016</b>
Distance to perennial watercourses (m)	1734.2 $\pm$ 271.4	2382.9 $\pm$ 122.1	1237.2 $\pm$ 86.4	1476.1 $\pm$ 53.4	-1.32	0.188	-1.24	0.215
Distance to non-perennial watercourses (m)	262.4 $\pm$ 37.9	351.5 $\pm$ 18.1	216.0 $\pm$ 65.4	355.4 $\pm$ 24.2	-1.17	0.241	-1.53	0.126
Distance to nearest dams (m)	1379.6 $\pm$ 348.2	1980.5 $\pm$ 151.7	714.3 $\pm$ 53.4	1088.7 $\pm$ 84.8	-1.31	0.191	-1.36	0.173
Distance to cleared land >10 ha (m)	303.0 $\pm$ 41.0	484.2 $\pm$ 31.6	472.7 $\pm$ 61.1	470.5 $\pm$ 24.1	-1.57	0.117	-0.13	0.898
Distance to nearest gap or shelterwood	81.2 $\pm$ 19.5	74.2 $\pm$ 8.9	82.3 $\pm$ 17.8	75.2 $\pm$ 9.2	0.50	0.672	0.45	0.646

<sup>a</sup> Ordinal variables, all others are continuous.

<sup>b</sup> Random jarrah trees (n = 118); random marri trees (n = 86). The number of roost trees is the same as at the local scale.

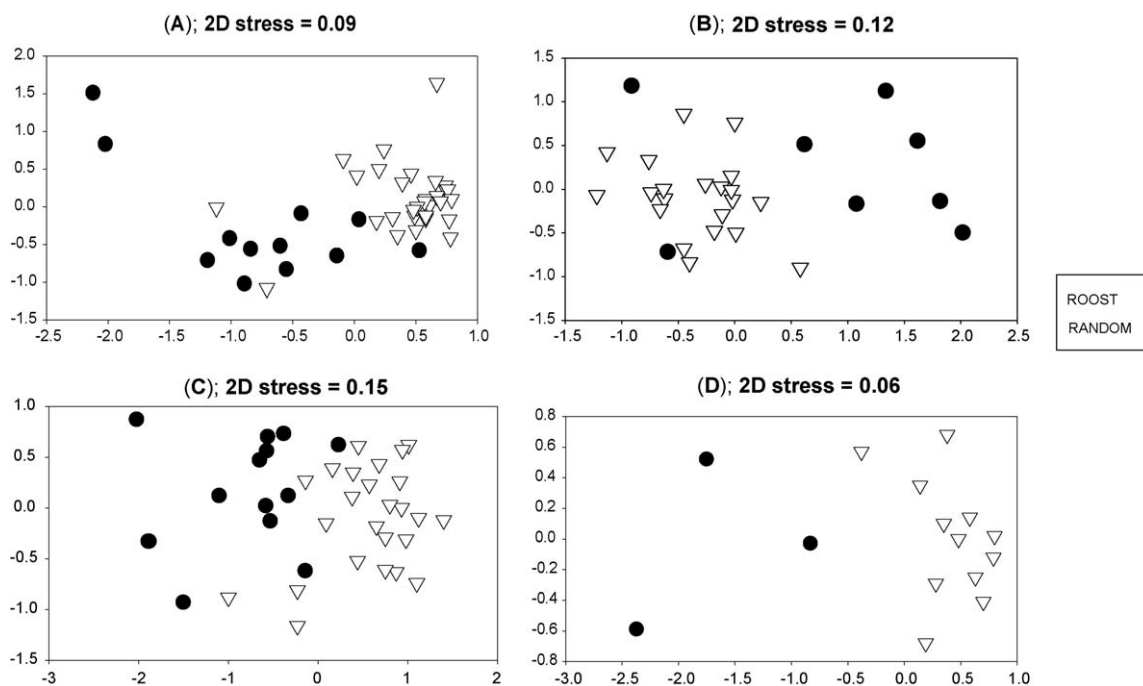
**Table 5**  
Differences among continuous and ordinal variables between roosts that were used as roost sites by southern forest bats (*Vespadelus regulus*; n = 10) and those used by Gould's long-eared bat (*Nyctophilus gouldi*; n = 11), at the focal-roost level and in the surrounding plots in the jarrah forests, south-western Australia, February–March 2009. Significant results are shown in bold.

Variable	Jarrah		Marri		Test statistic <sup>a</sup>			
	<i>V. regulus</i> (n = 18)	<i>N. gouldi</i> (n = 14)	<i>V. regulus</i> (n = 3)	<i>N. gouldi</i> (n = 8)	Jarrah		Marri	
					t <sub>30</sub>	P	t <sub>9</sub>	P
Tree characteristics								
DBHOB (cm)	89.5 $\pm$ 7.4	78.0 $\pm$ 7.4	88.6 $\pm$ 21.2	63.3 $\pm$ 8.9	-0.50	0.629	-1.19	0.252
Tree height (m)	33.3 $\pm$ 1.3	26.8 $\pm$ 2.7	32.4 $\pm$ 3.3	26.4 $\pm$ 3.5	-2.10	<b>0.045</b>	-0.91	0.385
Height relative to canopy height (%)	100.3 $\pm$ 3.9	87.7 $\pm$ 9.1	99.3 $\pm$ 5.4	85.6 $\pm$ 9.9	-1.59	0.122	-0.86	0.414
Roost entrance height (m)	23.2 $\pm$ 1.2	11.5 $\pm$ 1.0	22.9 $\pm$ 2.2	12.7 $\pm$ 1.5	-6.49	<b>&lt;0.001</b>	-2.63	<b>0.027</b>
Decay stage <sup>b</sup>	2.7 $\pm$ 0.2	3.3 $\pm$ 0.2	3.7 $\pm$ 0.3	3.3 $\pm$ 0.4	-1.84	0.066	0.36	0.722
Bark-cover class <sup>b</sup>	3.4 $\pm$ 0.1	3.0 $\pm$ 0.2	3.0 $\pm$ 1.0	3.4 $\pm$ 0.3	1.33	0.183	0.00	1.000
Crown senescence classification <sup>b</sup>	6.0 $\pm$ 0.5	6.8 $\pm$ 0.8	8.0 $\pm$ 1.5	6.3 $\pm$ 1.2	-0.96	0.338	0.73	0.465
Dead Branch Order (DBO) <sup>b</sup>	4.2 $\pm$ 0.3	4.6 $\pm$ 0.6	4.7 $\pm$ 0.3	5.0 $\pm$ 0.8	-0.41	0.682	-0.32	0.752
Site characteristics (extrinsic variables)								
Mean distance to nearest five available trees (m)	5.5 $\pm$ 0.3	5.6 $\pm$ 0.5	4.9 $\pm$ 1.3	5.2 $\pm$ 0.7	-0.20	0.841	0.26	0.801
Height of available nearest tree (m)	20.0 $\pm$ 1.2	24.4 $\pm$ 1.7	15.4 $\pm$ 3.0	24.4 $\pm$ 3.2	1.97	0.059	1.46	0.179
Mean canopy height (m)	33.3 $\pm$ 0.7	30.5 $\pm$ 0.7	32.5 $\pm$ 1.6	30.3 $\pm$ 1.8	-2.59	<b>0.015</b>	-0.70	0.502
Mean canopy cover	65.9 $\pm$ 2.1	60.8 $\pm$ 2.9	68.4 $\pm$ 8.3	64.8 $\pm$ 5.5	-1.44	0.160	-0.40	0.702
Sub-canopy index	24.2 $\pm$ 2.0	33.4 $\pm$ 3.4	13.3 $\pm$ 2.7	31.0 $\pm$ 4.2	2.39	<b>0.023</b>	2.85	<b>0.019</b>
Canopy index	31.7 $\pm$ 2.7	41.5 $\pm$ 3.0	30 $\pm$ 8.7	46.9 $\pm$ 1.9	2.06	<b>0.048</b>	2.88	<b>0.018</b>
Slope (degrees)	2.63 $\pm$ 0.5	3.36 $\pm$ 0.5	1.00 $\pm$ 0.00	4.00 $\pm$ 0.7	1.39	0.176	1.27	0.142
Elevation (m)	206.28 $\pm$ 7.1	221.07 $\pm$ 8.3	199.73 $\pm$ 19.5	241.76 $\pm$ 5.5	1.53	0.137	1.48	0.130
Distance to nearest water point (m)	711.38 $\pm$ 61.7	492.29 $\pm$ 30.0	608.00 $\pm$ 225.7	416.36 $\pm$ 49.5	-3.14	<b>0.004</b>	-4.12	<b>0.005</b>
Distance to perennial watercourses (m)	2131.24 $\pm$ 175.6	1734.16 $\pm$ 271.4	2152.57 $\pm$ 318.2	1237.19 $\pm$ 86.4	-1.92	0.065	-3.50	<b>0.007</b>
Distance to non-perennial watercourses (m)	256.75 $\pm$ 34.6	262.35 $\pm$ 37.9	173.84 $\pm$ 160.5	216.00 $\pm$ 65.4	0.26	0.796	1.42	0.106
Distance to nearest dams (m)	1988.64 $\pm$ 285.8	1379.56 $\pm$ 348.2	2350.42 $\pm$ 599.7	714.34 $\pm$ 53.4	-2.02	0.053	-5.39	<b>0.001</b>
Distance to cleared land >10 ha (m)	489.13 $\pm$ 82.4	303.01 $\pm$ 41.0	360.91 $\pm$ 206.2	472.67 $\pm$ 61.1	-1.27	0.215	1.54	0.157
Distance to nearest gap or shelterwood (m)	194.1 $\pm$ 43.1	83.6 $\pm$ 20.4	213.9 $\pm$ 44.9	81.6 $\pm$ 18.7	-1.12	0.274	-1.46	0.177

<sup>a</sup> Two-sampled t-test, with comparisons for corresponding tree species, jarrah against jarrah (d.f. = 29) and marri against marri (d.f. = 9).

<sup>b</sup> Ordinal variables, all others are continuous. Ordinal variables were compared using Mann–Whitney U-tests, with Z-adjusted as the test statistic





**Fig. 2.** Two-dimensional ordination (semi-strong hybrid multidimensional scaling ordination) based on measured variables of roost and random trees for *N. gouldi* [A (jarrah; ANOSIM Global test statistic,  $R=0.64$ ;  $P=0.001$ ); B (marri; ANOSIM Global test statistic,  $R=0.67$ ;  $P=0.001$ )] and *V. regulus* [C (jarrah; ANOSIM Global test statistic,  $R=0.51$ ;  $P=0.001$ ) and D (marri; ANOSIM Global test statistic,  $R=0.94$ ;  $P=0.002$ )].

observations on roost–site preferences of the two species at the two locations may be influenced by the social behaviour of related individuals belonging to a social group. However, the influence of social behaviour may be minimal given that the bats were captured at two spatially distant waterholes located in areas with different logging histories at different times in February and March 2009. Moreover, our results share strong similarities to other studies of bat roosts in Australia, further suggesting that social behaviour did not strongly bias our results.

Despite the limitations of our data, this study revealed noteworthy results in the choice of roost sites in a logged jarrah forest landscape in south-western Australia. Radio-tracked bats showed both inter-specific similarities and differences in the choice of roost trees and sites. While both bat species generally selected trees with large diameters, *V. regulus* roosted exclusively in hollows in tall trees, with 86% of all roosts occurring in jarrah and the rest in marri trees. This is consistent with other studies that have found a range of Australian bat species are dependant on *Eucalyptus* hollows (e.g. Lunney et al., 1985; Tidemann and Flavel, 1987; Taylor and Savva, 1988), including exclusive use of hollows as roosts by *Vespardelus pumilus* in *Eucalyptus* forests of northern NSW, Australia (Law and Anderson, 2000), and *Vespardelus vulturnus* within a remnant woodland on Phillip Island, Australia (Campbell et al., 2005). Collectively this and other studies highlight the importance of tree cavities as roost sites for bats of the genus *Vespardelus* in Australia.

Compared to *V. regulus*, tree height was not an important factor for *N. gouldi*, which used a broader range of roost types including hollows, exfoliating bark, cracks and balga skirts. The use of many roost types by *N. gouldi* in this study is consistent with previous studies on *Nyctophilus geoffroyi*, which roosted in hollows, under bark, fissures, cracks, buildings, posts and hanging clothes (Tidemann and Flavel, 1987; Lumsden et al., 2002a). In contrast to our study, 75% of *N. gouldi* roosts were found in tree hollows in a logged forest in New South Wales, Australia (Lunney et al., 1988). The difference between the two studies could be due to the difference in the sampling period. Our study was conducted in February and March only, whereas Lunney et al. (1988) sampled bats over

four different months, including the maternity season. Therefore, more observations on roost use throughout the year are required to comprehensively determine roost requirements for bats. Maternity roosts of *N. gouldi* and other Australian bats occur exclusively in tree hollows (e.g. Lunney et al., 1988; Law and Anderson, 2000), which likely partly explains the differences between the two studies. Therefore, more observations on roost use throughout the year are required to comprehensively determine roost requirements for bats, but we consider it likely that tree hollows are a critical resource for *N. gouldi*, particularly as maternity roosts.

Bats of both species selected trees with a mean DBHOB > 80 cm, which is consistent with those reported for other Australian bats (e.g. Lunney et al., 1988; Herr and Klomp, 1999; Law and Anderson, 2000; Lumsden et al., 2002a) and, as reported by many studies elsewhere, roost trees were significantly larger than random trees. These findings add to available evidence that older and large mature trees are important roost sites for bats (e.g. Sedgeley and O'Donnell, 1999; Lumsden et al., 2002a; Kalcounis-Rüppell et al., 2005). In addition, both species frequently used roosts in trees at intermediate or advanced stages of decay, crown senescence and deterioration with a lower percent bark cover than random trees. Larger trees generally contain larger and more hollows (e.g. Gibbons et al., 2000; Whitford and Williams, 2002) and potentially thicker decorticating bark with better thermal properties that offer better protection from inclement weather and predators (Sedgeley, 2001; Kunz and Lumsden, 2003). However, Turbill (2006) found male *N. gouldi* can save energy by roosting in exposed locations under bark and using passive warming from solar radiation to arouse themselves from torpor, which may explain their reduced reliance on hollows in this study.

We found inter-specific differences in the choice of roost sites with respect to vegetation structure and canopy cover. While *N. gouldi* selected roosts closer to vegetation with a higher canopy cover, *V. regulus* roosts were located in more open habitat with less canopy cover. In addition, hollow entrances of *V. regulus* were high ( $\geq 22$  m) above ground. In contrast, roost entrances of *N. gouldi* were within 13 m above ground and the species tended to locate roosts

in structurally complex and cluttered vegetation with higher overstorey tree densities and more midstorey and understorey trees than *V. regulus* (Table 5). Mature forest and unlogged buffers in this study were relatively open and had less understory and midstorey vegetation compared to the more closed and dense young regrowth. The differences between the two bat species in the choice of roost sites with respect to roost entrance height and closeness to vegetation may have been due to their differential levels of clutter tolerance (Table 5). *N. gouldi* is typically a clutter tolerant species because of its low aspect ratio and wing loading that allows slow flight and high manoeuvrability in dense vegetation (Fullard et al., 1991). In contrast, *V. regulus* bats have an intermediate aspect ratio and wing loading and are not well adapted for highly manoeuvrable flight (O'Neill and Taylor, 1986). This may explain their preference for roosting in the more open mature forest and riparian buffers, while avoiding the more closed, dense young regrowth. Open forest may also be favoured for roosting because its structure allows more direct sunlight on tree trunks and canopies, which may confer thermal advantages for developing young (Racey and Swift, 1981; Turbill and Geiser, 2005). Alternatively, the more open forest conditions could be an indicator of forest age, with mature forest providing more roosting opportunities resulting from many large diameter trees with more hollows.

#### 4.2. Mature forest and riparian buffers as roost sites for bats

Both species relied heavily on buffers for roosting, although *V. regulus* roosted further from creek lines than *N. gouldi*. Buffers were contemporarily unharvested forests (i.e. >30 years unlogged, and lightly selectively harvested when previously done so) retained adjacent to gap release cells (i.e. TEAS – temporary exclusion area system) and around ephemeral drainage lines and streams (i.e. riparian zones). Therefore the use of these areas was likely due to their structure and placement in the landscape rather than the presence of water (Perry et al., 2007). The location of 95% of roosts used by *V. regulus* in mature forest and buffers during this study was significantly greater than was randomly available within the study area, indicating a strong preference for these stands. In contrast, *N. gouldi* appeared to prefer forests that have been logged since 1985.

As in other studies, individual bats of both species changed roosts often, moving to a new roost every 1–2 days, but displayed fidelity to a general area. Bats of both species generally preferred roosting in older forest, probably because these forests provided sufficient alternate roosts required for long-term use (Lumsden et al., 2002a). The mature and/or uncut forest contained a much higher density of trees with hollows (16–32 trees ha<sup>-1</sup>) compared to shelterwood creation and gap release sites (8–12 trees ha<sup>-1</sup>). Mature forest hollow tree densities are comparable to average densities of live and dead hollow trees of 17 and 18 ha<sup>-1</sup> for *Chalinolobus gouldii* and *N. geoffroyi* roost areas, respectively in a fragmented landscape in south-eastern Australia, while the densities in the shelterwood and gap release stands were similar to the 11 ha<sup>-1</sup> in 'available habitat' where these bats were not found to roost in south-eastern Australia (Lumsden et al., 2002b). These results are consistent with other studies that found most bats prefer older forest stands or mature forests in Australia (e.g. Lunney et al., 1988; Taylor and Savva, 1988; Law and Anderson, 2000; Lumsden et al., 2002a), and elsewhere in temperate forests (e.g. Brigham et al., 1997; Crampton and Barclay, 1998; Sedgeley and O'Donnell, 1999). However, where older forest is absent, *V. pumilus* maintains similar colony sizes in the scarce roosts remaining within regrowth forest (Law and Anderson, 2000). At present, it is unknown what roosts would be used by jarrah forest bats in areas where mature forest is locally scarce.

*N. gouldi* bats selected roosts closer to water holes than was randomly expected. The water holes are typically artificial water

points, used as water sources for fire suppression, and were distributed throughout the forest. Two factors might explain the bats' preference for roosting closer to water holes. First, it would reduce the time and energy spent commuting to the water points for drinking and/or foraging for insect prey over water (Lewis, 1995; Kunz and Lumsden, 2003; Fukui et al., 2006). Secondly, being lower in the landscape, these areas generally coincided with riparian buffers, which contained many large diameter trees with hollows hence greater roosting opportunities.

The two bat species used retained habitat trees in gap release and shelterwood creation silvicultural treatments as roost sites, but this was very infrequent in *V. regulus*. Further studies are required to demonstrate if these retained trees can be used effectively by viable populations of bats, especially in the absence of unlogged mature forest and riparian buffers, but our results suggest this would be unlikely, at least for *V. regulus*. Given the dependence of jarrah forest bats on tree hollows as maternity roosts, studies examining the use of retained habitat trees as roosts during the maternity season are critical in understanding the value of retained trees in helping maintain bat populations in production forests.

Current guidelines for jarrah forest harvesting involve retention of five primary habitat trees ha<sup>-1</sup> and six–eight secondary habitat trees ha<sup>-1</sup> in areas cut to gap, shelterwood or 'selective cut in dieback' (CCWA, 2004). Between 1996 and 2003 there were provisions for four primary habitat trees plus six–eight secondary habitat trees (if present) (Silviculture Guideline 1/95). Prior to this it was 15 trees per 5 ha (Silviculture specification 5/89). While these improvements in the number of retained, actual and potential, habitat trees are important for the long-term maintenance of roost sites for bats in logged jarrah forests, it is unclear whether these measures are sufficient and, therefore, should be a subject for future studies, as discussed above. Indeed, they are much lower than the hollow tree density reported by Lumsden et al. (2002b) in a fragmented landscape in south-eastern Australia, but they are similar to densities in a regrowth forest growing on lower slopes in northern NSW (Law and Anderson, 2000). Although the retention and sustained recruitment of large mature trees at various stages of decay in logged forests is essential for the long-term maintenance of roost sites for bats and other hollow-dependent fauna into the future, the presence of retained habitat (unlogged buffers and old-growth forest) appears more important, indicating that a consideration of the area retained at a landscape scale is crucial.

The logging rotation in the jarrah forests is dependent on a 10-year forest management plan (FMP), with the current FMP ending in 2014. At two forest blocks, Kingston and Warrup, where our study was undertaken, approximately 54% of the total area (11,740 ha) is currently reserved from logging as conservation reserves, informal reserves (riparian buffers, diverse ecotype zones, road reserves), old-growth forest, and fauna habitat zones. Of these, only about 39% are permanently reserved (including riparian buffers) from logging in the future. Most of the study area had experienced at least one cycle of harvesting between the 1920s and 1979, typically in a very selective manner that still retained many mature elements of the original forest. Currently, at least 6% has no evidence of being previously cut and since 1980; approximately 20% of the study area has been harvested, generally for the second time. The remaining 26% of the study area available for harvesting may potentially be harvested in coming decades, in addition to follow-up silvicultural treatment in the post 1980 harvest areas (CCWA, 2004). Thus, many jarrah forest areas have already been selectively logged, and with increasing pressure on remaining areas of forest that will be logged during the second rotation, it is uncertain whether jarrah forest logging will retain sufficient habitat containing multiple old hollow-bearing trees required for many roosting bat species and other hollow-nesting fauna.

## 5. Conclusions

Our study reveals some important implications for the management of bat roost sites. The two bat species chose different roosts insofar as level of clutter, height and location in the landscape was concerned. While *N. gouldi* selected roosts at sites with more clutter, *V. regulus* roosts were located in open areas of mature forest and riparian buffers. Although gap release and shelterwood creation sites retained tall and large diameter hollow-bearing trees that were less cluttered than surrounding vegetation, bats, especially *V. regulus*, avoided locating roosts in such treatments when older forest was available nearby. In general, remnant trees, including retained habitat trees, in these silvicultural treatments were not preferred by both bat species as roost sites during late summer and early autumn and further studies are required to investigate if they are used successfully by breeding bats when old forest is absent or less accessible. Given the high rates of roost switching and the variety of roost sites used by bats, it is essential that multiple roosts are maintained and continually recruited in the forest to satisfy bat roosting requirements (Willis and Brigham, 2004).

Our study demonstrated the importance of unharvested buffers surrounding ephemeral streams, and more open mature forests, with relatively open understoreys, as roosting habitats for both *V. regulus* and *N. gouldi*, probably because they provided a large pool of older and mature trees in a variety of decay classes as roost sites. In this regard, provisions since 2004 for Fauna Habitat Zones (i.e. >200 ha areas with mature forest structure generally interspersed 2–4 km apart within areas available for logging (Conservation Commission, 2004, FMP 2004–2013) are likely to benefit bats, particularly those that rely on blocks of forest that maintain mature forest attributes or characteristics. Notably, our study provides only a snapshot of bat habitat use and preferences. Serious management consideration should also be given to foraging habitat, and overwintering and maternity roost sites (Sedgely, 2001; Kunz and Lumsden, 2003; Lumsden et al., 2002a). While logging impacts on bat activity including foraging activity is examined elsewhere (PWW, unpublished data), targeted research on temporal/seasonal differences in roost use needs to be undertaken in the jarrah forests of south-western Australia.

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## References

- Abbott, I., Loneragan, O.W., 1986. The ecology of jarrah (*Eucalyptus marginata*) in the northern jarrah forest of Western Australia. Western Australian Department of Conservation and Land Management, Bulletin No. 1.
- Abbott, I., Whitford, K., 2002. Conservation of vertebrate fauna using hollows in forests of south-west Western Australia: strategic risk assessment in relation to ecology, policy, planning and operations management. Pacific Conservation Biology 7, 240–255.
- Aldridge, H.D.J.N., Brigham, R.M., 1988. Load carrying and manoeuvrability in an insectivorous bat - a test of 5 percent "rule" of Radiotelemetry. Journal of Mammalogy 69, 379–382.
- Ball, I.R., Lindenmayer, D.B., Possingham, H.P., 1999. A tree hollow dynamics simulation model. Forest Ecology and Management 123, 179–194.
- Bradshaw, F.J., 1999. Trends in silvicultural practices in the native forests of Western Australia. Australian Forestry 62, 255–264.
- Brigham, R.M., Fenton, M.B., 1986. The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64, 1128–1133.
- Brigham, R.M.R., Vonhof, M.J., Barclay, R.M.R., Gwilliam, J.C., 1997. Roosting behaviour and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). Journal of Mammalogy 78, 1231–1239.
- Campbell, S., Lumsden, L.F., Kirkwood, R., Coulson, G., 2005. Day roost selection by little forest bats (*Vespadelus vulturinus*) within remnant woodland on Phillip Island, Victoria. Wildlife Research 32, 183–191.
- Churchill, 2008. Australian Bats, second ed. NSW, Australia.
- Commonwealth of Australia and Western Australian Government, 1998. Comprehensive Regional Assessment – A Regional Forest Agreement for Western Australia. Commonwealth of Australia and Western Australian Regional Forest Agreement Steering Committee, Perth, Western Australia.
- Conservation Commission of Western Australia, 2004. Forest Management Plan 2004–2013. Conservation Commission of Western Australia, Perth.
- Conservation Commission of Western Australia, 2003. Implementing Ecologically Sustainable Forest Management: an Explanatory Paper by the Conservation Commission of Western Australia to accompany the Forest Management Plan 2004–2013. Conservation Commission of Western Australia, Perth.
- Crampton, L.H., Barclay, R.M.R., 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. Conservation Biology 12, 1347–1358.
- Day, R.W., Quinn, G.P., 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59, 433–463.
- Fukui, D., Murakami, M., Nakano, S., Aoi, T., 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75, 1252–1258.
- Fullard, J.H., Koehler, C., Surlykke, A., McKenzie, N.L., 1991. Echolocation ecology and flight morphology of insectivorous bats (Chiroptera) in south-western Australia. Australian Journal of Zoology 39, 427–438.
- Gentili, J., 1989. Climate of the Jarrah forest. In: Dell, B., Havel, J.J., Malajczuk, N. (Eds.), The Jarrah Forest: A Complex Mediterranean Ecosystem. Kluwer Academic Publishers, USA, pp. 23–40.
- Gibbons, P., Cunningham, R.B., Lindenmayer, D.B., 2008. What factors influence the collapse of trees retained on logged sites? A case control study. Forest Ecology and Management 255, 62–67.
- Gibbons, P., Lindenmayer, D.B., 2002. Tree Hollows and Wildlife Conservation in Australia. CSIRO Publishing, Melbourne.
- Gibbons, P., Lindenmayer, D.B., Barry, S.C., Tanton, M.T., 2000. The formation of hollows in eucalypts from temperate forests. Pacific Conservation Biology 6, 218–228.
- Goldingay, R.L., 2009. Characteristics of tree hollows used by Australian birds and bats. Wildlife Research 36, 394–409.
- Havel, J.J., 1975. Site-vegetation mapping in the northern jarrah forest (Darling Range). 1. Definition of site-vegetation types. Forests Department Western Australia Bulletin 86, Perth, Western Australia.
- Havel, J.J., 1975. Site-vegetation mapping in the northern jarrah forest (Darling Range). 2. Location and mapping of site-vegetation types. Forests Department Western Australia Bulletin 87, Perth, Western Australia.
- Herr, A., Klomp, N.I., 1999. Preliminary investigation of roosting habitat preferences of the large forest bat *Vespadelus darlingtoni* (Chiroptera, Vespertilionidae). Pacific Conservation Biology 5, 208–213.
- Hosken, D.J., 1996. Roost selection by the lesser long-eared bat, *Nyctophilus geoffroyi*, and the greater long-eared bat, *N. major* (Chiroptera: Vespertilionidae) in Banksia woodlands. Journal of the Royal Society of Western Australia 79, 211–216.
- Hutson, A.M., Mickleburgh, S.P., Racey, P.A. (Eds.), 2001. Microchiropteran Bats: Global Status Survey and Conservation Action Plan. [International Union for Conservation of Nature Species Survival Commission (IUCN/SSC)]. Chiroptera Specialist Group, Gland, Switzerland.
- Kalcounis-Rüppell, M.C., Psyllakis, J.M., Brigham, R.M., 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. Wildlife Society Bulletin 33, 1123–1132.
- Kunz, T.H., 1982. Ecology of Bats. Plenum Publishing, New York, USA.
- Kunz, T.H., Lumsden, L.F., 2003. Ecology of cavity and foliage roosting bats. In: Kunz, T.H., Fenton, B. (Eds.), Bat Ecology. The University of Chicago Press, Chicago and London, pp. 3–89.
- Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L., Lovejoy, T.E., 2000. Rainforest fragmentation kills big trees. Nature 404, 836.
- Law, B.S., 1996. The ecology of bats in south-east Australian forests and potential impacts of forestry practises: a review. Pacific Conservation Biology 2, 363–374.
- Law, B.S., 2004. Challenges of managing bats in the State forests of New South Wales. In: Lunney, D. (Ed.), Conservation of Australia's Forest Fauna, second ed. Royal Zoological Society of New South Wales, Mosman, NSW, Australia, pp. 748–760.
- Law, B.S., Anderson, J., 2000. Roost preferences and foraging ranges of the eastern forest bat *Vespadelus pumilus* under two disturbance histories in northern New South Wales, Australia. Austral Ecology 25, 352–367.

- Law, B.S., Chidel, M., 2002. Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *Journal of Applied Ecology* 39, 605–617.
- Lewis, S.E., 1995. Roost fidelity of bats: a review. *Journal of Mammalogy* 76, 481–496.
- Lewis, S.E., 1996. Low roost-site fidelity in pallid bats: associated factors and effect on group stability. *Behavioural Ecology Sociobiology* 39, 335–344.
- Lindenmayer, D.B., Franklin, J.F., 2002. *Conserving Forest Biodiversity: A Comprehensive Multi-Scaled Approach*. Island Press, Washington, DC.
- Lindenmayer, D.B., Franklin, J.F. (Eds.), 2003. *Towards Forest Sustainability*. CSIRO Publishing, Melbourne.
- Lindenmayer, D.B., Claridge, A.W., Gilmore, A.M., Michael, D., Lindenmayer, B.D., 2002. The ecological roles of logs in Australian forests and the potential impacts of harvesting intensification on log-using biota. *Pacific Conservation Biology* 8, 121–140.
- Lloyd, A., Law, B., Goldingay, R., 2006. Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biological Conservation* 129, 207–220.
- Lumsden, L.F., Bennett, A.F., Silins, J.E., 2002a. Selection of roost sites by the lesser long-eared bat (*Nyctophilus geoffroyi*) and Gould's wattled bat (*Chalinobolus gouldii*) in south-eastern Australia. *Journal of Zoology* 257, 207–218.
- Lumsden, L.F., Bennett, A.F., Silins, J.E., 2002b. Location of roosts of the lesser long-eared bat *Nyctophilus geoffroyi* and the Gould's wattled bat *Chalinobolus gouldii* in a fragmented landscape in south-eastern Australia. *Biological Conservation* 106, 237–249.
- Lunney, D., Matthews, A., 2004. Conserving the forest mammals of New South Wales. In: Lunney, D. (Ed.), *Conservation of Australia's forest fauna*, second ed. Royal Zoological Society of New South Wales, Mosman, pp. 988–1021.
- Lunney, D., Barker, J., Priddel, D., 1985. Movements and day roosts of the Chocolate-wattled Bat. *Chalinobolus morio* (Gray) (Microchiroptera: Vespertilionidae) in a logged forest. *Australian Mammalogy* 8, 313–317.
- Lunney, D., Barker, J., Priddel, D., O'Connell, M., 1988. Roost selection by Gould's long-eared bat. *Nyctophilus gouldii* Tomes (Chiroptera: Vespertilionidae), in logged forest on the south coast of New South Wales. *Australian Wildlife Research* 15, 375–384.
- Lunney, D., Barker, J., Leary, T., Priddel, D., Wheeler, R., O'Connor, P., Law, B., 1995. Roost selection by the north Queensland long-eared bat *Nyctophilus bifax* in littoral rainforest in the Iluka World Heritage Area, New South Wales. *Australian Journal of Ecology* 20, 532–537.
- Mackowski, C., 1984. The ontogeny of hollows in blackbutt (*Eucalyptus pilularis*) and its relevance to the management of forests for possums, gliders and timber. In: Smith, A., Hume, A.I. (Eds.), *Possums and Gliders*. Surrey Beatty and Sons, Sydney, NSW, pp. 553–567.
- Maser, C., Anderson, R.G., Cromak, K., Williams, J.T., Martin, R.E., 1979. Dead and downed woody material. In: Thomas, J.W. (Ed.), *Wildlife Habitats in Managed Forests – the Blue Mountains of Oregon and Washington*. Agric. Handb. 533. U.S. Department of Agriculture, Washington, DC, pp. 78–95.
- Oliveira, M.A., Santos, A.M.M., Tabarelli, M., 2008. Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. *Forest Ecology and Management* 256, 1910–1917.
- O'Neill, M.G., Taylor, R.J., 1986. Observations on flight patterns and foraging behaviour of Tasmanian bats. *Australian Wildlife Research* 13, 427–432.
- Parnaby, H., Hamilton-Smith, E., 2004. The remarkable "Adaptable Bat": a challenge to ecological concepts in the management of Australian forest bats. In: Lunney, D. (Ed.), *Conservation of Australia's Forest Fauna*, second ed. Royal Zoological Society of New South Wales, Mosman, NSW, Australia, pp. 81–93.
- Perry, R.W., Thill, R.E., Leslie, D.M., 2007. Selection of roosting habitat by forest bats in a diverse forested landscape. *Forest Ecology and Management* 238, 156–166.
- Racey, P.A., 1988. Reproductive assessment in bats. In: Kunz, T.H. (Ed.), *Ecological and Behavioural Methods for the Study of Bats*. Smithsonian Institution Press, Washington, D.C., USA, pp. 31–45.
- Racey, P.A., Swift, S.M., 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *Journal of Reproductive Fertility* 61, 123–129.
- Rhodes, M., Wardell-Johnson, G., 2006. Roost tree characteristics determine use by the white-striped freetail bat (*Tadarida australis*, Chiroptera: Molossidae) in suburban subtropical Brisbane, Australia. *Austral Ecology* 31, 228–239.
- Rydell, J., Entwistle, A., Racey, P.A., 1996. Timing of foraging flights of three species of bats in relations to insect activity and predation risk. *Oikos* 76, 243–252.
- Schulz, M., 2000. Roosts used by the Golden-tipped bat, *Kerivoula papuensis* (Chiroptera: Vespertilionidae). *Journal of Zoology (London)* 250, 467–478.
- Sedgeley, J.A., 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinobolus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38, 425–438.
- Sedgeley, J.A., O'Donnell, C.F.J., 1999. Roost selection by the long-tailed bat, *Chalinobolus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. *Biological Conservation* 88, 261–276.
- Smith, C.Y., Warkentin, I.G., Moroni, M.T., 2008. Snag availability for cavity nesters across a chronosequence of post-harvest landscapes in western Newfoundland. *Forest Ecology and Management* 256, 641–647.
- Stoneman, G.L., Borg, H., Rose, P.W., 1989. Recovery of vegetation cover following logging and regeneration in the southern forest of Western Australia and the short term hydrologic implications. *Australian Forestry* 52, 4–9.
- Taylor, R.J., Savva, N.M., 1988. Use of roost trees by four species of bats in state forest in south-eastern Tasmania. *Australian Wildlife Research* 15, 637–645.
- Tidemann, C.R., Flavel, S.C., 1987. Factors affecting choice of diurnal roost site by tree-hole bats (Microchiroptera) in south-eastern Australia. *Australian Wildlife Research* 14, 459–473.
- Turbill, C., 2006. Roosting and thermoregulatory behaviour of male Gould's long-eared bats. *Nyctophilus gouldii*: energetic benefits of thermally unstable tree roosts. *Australian Journal of Zoology* 54, 57–60.
- Turbill, C., Geiser, F., 2005. Thermal physiology of pregnant and lactating female and male long-eared bats, *Nyctophilus geoffroyi* and *N. gouldii*. *Journal of Comparative Physiology B* 176, 165–172.
- Turbill, C., Law, B.S., Geiser, F., 2003. Summer torpor in a free-ranging bat from subtropical Australia. *Journal of Thermal Biology* 28, 223–226.
- Vonhof, M.J., Barclay, R.M.R., 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology* 74, 1797–1805.
- Vonhof, M.J., Gwilliam, J.C., 2007. Intra- and interspecific patterns of day roost selection by three species of forest-dwelling bats in Southern British Columbia. *Forest Ecology and Management* 252, 165–175.
- Whitford, K.R., 2002. Hollows in Jarrah (*Eucalyptus marginata*) and Marri (*Corymbia calophylla*) trees. *Forest Ecology and Management* 160, 201–214.
- Whitford, K., Stoneman, G., 2004. Management of tree hollows in the jarrah *Eucalyptus marginata* forest of Western Australia. In: Lunney, D. (Ed.), *Conservation of Australia's Forest Fauna*, second ed. Royal Zoological Society of New South Wales, Mosman, NSW, Australia, pp. 807–829.
- Whitford, K.R., Williams, M.R., 2002. Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees – II. Selecting trees to retain for hollow dependent fauna. *Forest Ecology and Management* 160, 215–232.
- Willis, C.K.R., Brigham, R.M., 2004. Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Animal Behaviour* 68, 495–505.