

## Roost use by long-tailed bats in South Canterbury: examining predictions of roost-site selection in a highly fragmented landscape

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**Abstract:** We studied the roosting ecology of the long-tailed bat (*Chalinolobus tuberculatus*) during the spring-autumn months from 1998–2002 at Hanging Rock in the highly fragmented landscape of South Canterbury, South Island, New Zealand. We compared the structural characteristics and microclimates of roost sites used by communally and solitary roosting bats with those of randomly available sites, and roosts of *C. tuberculatus* occupying unmodified *Nothofagus* forest in the Eglinton Valley, Fiordland. Roosting group sizes and roost residency times were also compared. We followed forty radio-tagged bats to 94 roosts (20% in limestone crevices, 80% in trees) at Hanging Rock. Roosts were occupied for an average of 1 day and 86% were only used once during the study period. Colony size averaged  $9.8 \pm 1.1$  bats (range 2–38) and colonies were dominated by breeding females and young. Indigenous forest, shrubland remnants and riparian zones were preferred roosting habitats. Communally roosting bats selected roosts in split trunks of some of the largest trees available. Selection of the largest available trees as roost sites is similar to behaviour of bat species occupying unmodified forested habitats. Temperatures inside 12 maternity roosts measured during the lactation period were variable. Five roosts were well insulated from ambient conditions and internal temperatures were stable, whereas the temperatures inside seven roosts fluctuated in parallel with ambient temperature. Tree cavities used by bats at Hanging Rock were significantly nearer ground level, had larger entrance dimensions, were less well insulated, and were occupied by fewer bats than roosts in the Eglinton Valley. These characteristics appear to expose their occupants to unstable microclimates and to a higher risk of threats such as predation. We suggest that roosts at Hanging Rock are of a lower quality than those in the Eglinton Valley, and that roost quality may be one of the contributory factors in the differential reproductive fitness observed in the two bat populations. The value of introduced willows (especially *Salix fragilis*) as bat roosts should be acknowledged. We recommend six conservation measures to mitigate negative effects of deterioration of roosting habitat: protection and enhancement of the quality of existing roosts, replanting within roosting habitat, provision of high quality artificial roosts, predator control, and education of landowners and statutory bodies.

**Keywords:** bats; *Chalinolobus tuberculatus*; habitat fragmentation; roost-site selection.

## Introduction

Clearance and fragmentation of forests pose significant threats to invertebrates, amphibians, reptiles, birds and mammals [reviewed in Bennett (1999)]. The ecological consequences of habitat fragmentation are diverse, but are generally negative for obligate forest-dwellers and species that depend on old-age trees (O'Donnell, 1991). Negative effects include loss of species, increased impact of stochastic events, increases in edge effects, and reduction in population sizes because of greater isolation, reduced area of habitat, and reduced potential for migration into and out of fragments. Composition of faunal assemblages change, and fragmentation may benefit some species, while being detrimental to others

(Saunders *et al.*, 1991; Fahrig and Merriam, 1994; Weins, 1994).

The effects of fragmentation on forest-dwelling bats are equivocal, particularly in relation to their patterns of activity. Habitat use by bats is influenced by mechanical and perceptual constraints on flight, primarily in relation to wing morphology and echolocation call design (Norberg and Rayner, 1987; Fenton, 1990) and the structural complexity of habitats (McKenzie and Rolfe, 1986). Several studies have indicated that activity of bats increases when harvesting creates gaps and edges in forest, whereas others have indicated bat activity decreased in large openings and areas of clearcut (Brigham and Barclay, 1996; Krusic *et al.*, 1996). Other studies showed greater bat activity

occurred in older forest stands (Thomas, 1988; Hayes and Adam, 1996). It appears that the creation of gaps in forest will benefit bat species with moderate to fast flight speeds and limited manoeuvrability within dense vegetation by increasing availability of 'edge' foraging habitat.

In contrast, the effects of deforestation and deterioration in habitat quality on the composition of bat communities and on their roosting habitat appear unequivocal and are negative. Generally, species diversity values are much reduced in modified habitats and fewer numbers of total and rare bat species are found compared with undisturbed habitats (Brosset *et al.*, 1996; Medellín *et al.*, 2000). In unmodified forests, bats select the largest and oldest available trees in which to roost (Vonhof and Barclay, 1996; Menzel *et al.*, 1998; Rabe *et al.*, 1998; Sedgeley and O'Donnell 1999a). Tree harvesting, particularly selective logging that targets larger size classes of trees, will reduce the availability of preferred roosting habitat (Mackowski, 1984; Lindenmayer *et al.*, 1991). Studies of bats in managed forests showed that bats roosted in unmodified old-growth forest and seldom roosted in regenerating forest and clear-cut areas (Lunney *et al.*, 1988, Taylor and Savva, 1988; Crampton and Barclay, 1996).

New Zealand's extant bat fauna comprises two endemic species, the lesser short-tailed bat (*Mystacina tuberculata*) and the long-tailed bat (*Chalinolobus tuberculatus*) (Daniel, 1990). They are fully protected by the Wildlife Act (1953) and are categorised as 'Vulnerable' by the International Union for the Conservation of Nature (IUCN) (Hutson *et al.*, 2001). The most recent Department of Conservation threat classification system lists South Island *C. tuberculatus* as "Nationally Endangered" (Hitchmough, 2002).

Both bat species are closely associated with indigenous forest and depend almost exclusively on trees for roost sites (Daniel and Williams, 1984; Lloyd, 2001; O'Donnell, 2001). Peak foraging activity in *C. tuberculatus* occurs along forest edges (O'Donnell, 2000a) and *C. tuberculatus* populations have also been found in pine forests (Daniel, 1981) and in modified and agricultural landscapes (Daniel and Williams, 1984). In the predominantly pastoral landscapes of the western King Country and South Canterbury, *C. tuberculatus* has been reported roosting in a variety of sites in addition to trees; these included caves, limestone crevices and buildings (Daniel and Williams, 1981, 1983; Griffiths, 1996; O'Donnell, 2001). None of these roosts was known to be used by breeding bats.

Recently published research examined the roosting ecology of breeding colonies of *C. tuberculatus* in unmodified *Nothofagus* forest in the Eglinton Valley, Fiordland National Park. These bats roosted in small aggregations in well-insulated knot-hole cavities within red beech (*N. fusca*) trees that had distinctive structural

and microclimatic characteristics relative to those available (O'Donnell and Sedgeley, 1999; Sedgeley and O'Donnell, 1999a, 1999b). The authors hypothesised that the well-insulated roosts *C. tuberculatus* selected would improve this bat's breeding success and energy conservation in cold-temperate climates (Sedgeley, 2001). If we assume the large old-age trees used by bats in unmodified indigenous forest represent optimal high quality roost sites, we predict such roosts will be scarce in deforested landscapes, and bats may be forced to use roost sites of lower quality. The use of low quality roost sites is known to have negative effects on reproductive fitness and population viability in bats (Brigham and Fenton, 1986; Richter *et al.*, 1993; Zahn, 1999).

In this study we describe roost sites used by *C. tuberculatus* (including those used by breeding groups) in the highly fragmented and predominantly pastoral landscape at Hanging Rock, South Canterbury, New Zealand. Our objectives are to: (1) describe the physical structure of roosts at Hanging Rock and examine differences between those used by groups of communally roosting and solitary roosting bats; (2) examine whether bats at Hanging Rock select roost sites with distinctive characteristics as compared with available sites; (3) examine whether communally roosting bats at Hanging Rock select roost sites with similar characteristics to those used in an unmodified habitat in the Eglinton Valley, Fiordland; and (4) discuss the likely implications of roost-site selection for population viability and conservation of *C. tuberculatus* in modified and fragmented habitats.

## Methods and materials

### Study area

In pre-human times the downlands of South Canterbury in the South Island of New Zealand were thought to be covered in forests of matai (*Prumnopitys taxifolia*), kahikatea (*Dacrycarpus dacrydioides*), totara (*Podocarpus totara*), and trees such as tarata (*Pittosporum eugenioides*), broadleaf (*Griselinia littoralis*), fuchsia (*Fuchsia excorticata*) and fivefinger (*Pseudopanax arboreus*) (Leathwick *et al.*, 2001). These had been reduced to scattered remnants by the time of European settlement, and have further been reduced and degraded. Hanging Rock (170° 01'E, 44° 11'S) is 21 km south-west of the town of Geraldine (Fig. 1). The study area was centred on the Opihi River system and characterised by extensive limestone and sandstone bluffs and small areas of podocarp and mixed hardwood forest in a landscape dominated by pastoral land, exotic forestry plantations (primarily *Pinus radiata* and some *Eucalyptus* spp.) and exotic shrublands dominated by broom (*Cytisus scoparius*)

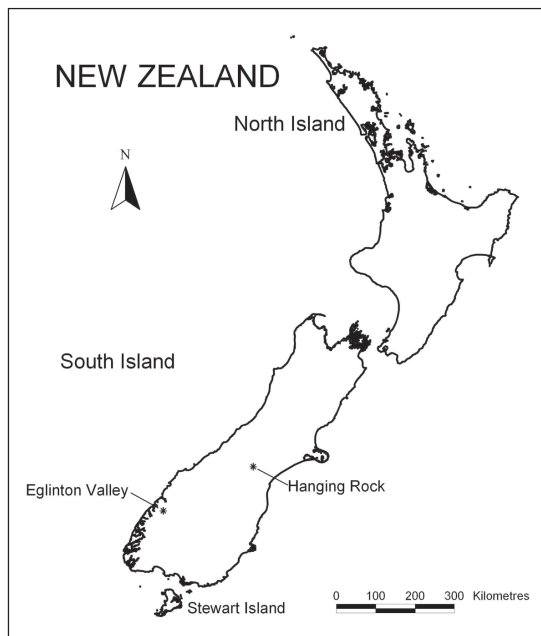


Figure 1. Location of study areas.

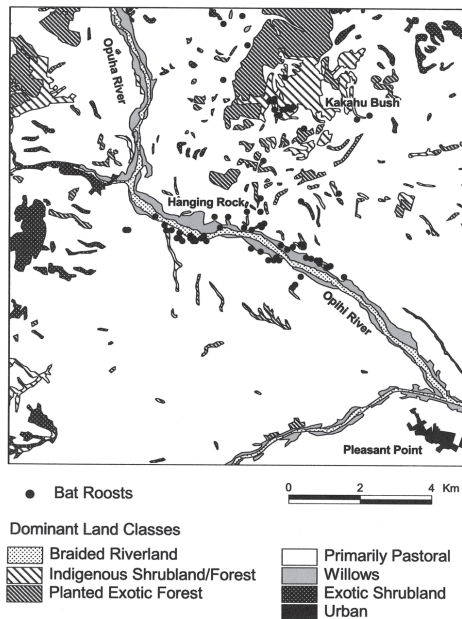


Figure 2. Map of the Hanging Rock study area illustrating dominant land classes and distribution of *Chalinolobus tuberculatus* roost sites, (n = 94) 1998–2002.

Table 1. Comparison of available habitat and habitat used for roosting by *Chalinolobus tuberculatus* at Hanging Rock (n = 94 roosts). Results expressed as proportions and habitat selection assessed using Bonferroni analysis and expressed as 95% Confidence Intervals (BCI).

Dominant land class	Area (ha)	Proportion of each habitat available	Proportion of bat roosts found in each habitat (with BCI)	Preference
Pastoral	23 972	0.828	0.372 (0.256–0.488)	Avoided
Planted exotic forest	1 644	0.057	0.043 (0–0.090)	Random
Riparian willows	872	0.030	0.319 (0.208–0.430)	Selected
Exotic shrubland	870	0.030	0	Not used
Indigenous shrubland	717	0.025	0.138 (0.082–0.220)	Selected
Braided riverbed	538	0.019	0	Not used
Indigenous forest remnants	219	0.008	0.128 (0.048–0.208)	Selected
Urban	102	0.003	0	Not used
Totals	28 934	1.00	1.00	

and gorse (*Ulex europaeus*). The riparian zones along the Opihi River have been extensively planted with non-native willow (mainly *Salix fragilis*), alder (*Alnus* spp.) and poplar (*Populus* spp.) to help prevent the flooding of the adjacent farmland (Fig. 2, Table 1).

Indigenous vegetation is limited to occasional remnants and scattered patches of regenerating shrublands predominated by cabbage trees (*Cordyline australis*), *Coprosma* spp., mahoe (*Melicytus ramiflorus*), and kanuka (*Kunzea ericoides*). The largest remnant is at Kakahu Bush (420 ha). This protected

area includes 87 ha of regenerating mixed podocarp/broadleaf forest, and large contiguous areas of kanuka-dominant shrubland and exotic shrubland that are being managed for regeneration. The forest has been cut-over during logging, but contains mature specimens of the original species including kahikatea, matai, totara, pokaka (*Eleocharpus hookerianus*), and associated sub-canopy species (J. Talbot, Trustee, South Canterbury Conservation Trust, Pleasant Point, N.Z., pers. comm.).

Annual rainfall averages 573 mm and mean monthly temperatures vary from 5.7°C in July to 16.2°C in January (National Institute of Water and Atmospheric Research Database).

### Capture of bats and location of roost trees

We studied *C. tuberculatus* over four years during spring to autumn months, 1998–2002. Roosts were found by following bats fitted with radio-transmitters (BD2A® 0.7 g transmitters, Holohil Systems, Carp, Ontario, Canada). Bats were caught in 4.2 m<sup>2</sup> harp-traps (specialised bat traps, Faunatech, Melbourne, Australia) set in bat fly-ways and foraging areas amongst riparian willows along the Ophi and Kakahu rivers. We radio-tracked a total of 4 adult males, 5 adult non-breeding females, 22 adult breeding females and 9 juveniles over the four field seasons. Transmitters were attached between the scapulae using a latex-based contact adhesive (Ados F2®, Ados Chemical Company, Auckland, N.Z.) after the fur had been partially trimmed with scissors. Bats were followed as long as transmitters were thought to be functioning. Roost sites were located during the day by radio-tracking using a TR4 receiver (Telonics, Arizona, U.S.A) and a 3-element hand-held yagi antenna (Sirtrack, Havelock North, N.Z.). We generally identified roost cavities by using the radio-receiver at close range and by the sounds of bats squeaking inside. Occasionally it was necessary to climb trees using a ladder or a single-rope technique (O'Donnell *et al.*, 1996) before using the radio-receiver at close range.

### Roosting behaviour

We used size and composition of roosting groups, roost residency times and levels of roost reuse as measures of roosting behaviour. One or two observers counted bats emerging from each roost at dusk. *Chalinolobus tuberculatus* is relatively easy to count since most leave roost sites while it is still light. On rare occasions when bats were still departing in darkness, or roosts were high in trees and visibility was poor, we used ultrasonic bat detectors (Batbox III®, Stag Electronics, Sussex, U.K.) to aid counts. Bats immediately left the vicinity of the roost and detectors picked up their echolocation signals clearly (O'Donnell and Sedgeley, 1999). We classified roosts as being occupied by either a solitary roosting bat, or by an aggregation of  $\geq 2$  bats, and describe them hereafter as either solitary or communal roosts. The composition of roosting groups of bats was determined by capturing bats as they emerged at dusk with harp traps positioned directly outside roost entrances (Sedgeley and O'Donnell, 1996; O'Donnell and Sedgeley, 1999). Age, sex and reproductive status of all bats caught were recorded. We defined adult breeding females as

those that were pregnant (determined by gentle palpation of the abdomen), lactating (identified by the presence of large nipples surrounded by bare skin) or post-lactating (large but regressing nipples, with some fur regrowth). Adult females with tiny nipples covered with fur were classified as non-breeding (either they had never given birth or had not done so recently). We classified males as sexually active when their epididymides were clear or grey and distended, and as inactive when they were black and regressed. Young-of-the-year were identified by unfused phalangeal epiphyses, and we classified them as juveniles (O'Donnell, 2002).

### Assessing roost-site selection

We assessed roost-site selection by comparing the characteristics of roosting habitat and roost trees with those of available sites within a c. 29 000 ha study area over which *C. tuberculatus* is known to range (N.Z. Map Series 260, Map J38). Available habitat types (= eight dominant land classes) were mapped from 1996 Landsat Satellite Imagery (Ministry of Forestry, unpublished data; Fig. 2). We sampled available trees along 50 one km transects that were randomly chosen from 110 km of roads throughout the study area. Roads were suitable transects because in this area fields were mostly clear of trees except along roadside margins. The road system was extensive and traversed all forest remnants and representative habitat types.

Sampling of random trees was limited to those that we considered to be potentially available to bats, i.e., if they were of a sufficient size and age to develop cavities [ $\geq 15$  cm stem diameter at breast height (DBH), adapted from Sedgeley and O'Donnell (1999a)]. The nearest available tree within 50 m of 10 sampling points at 100 m intervals was measured for each transect. Not all transects yielded 10 trees/transect, and the total number sampled was 348 trees. We also assessed random trees for presence of cavities available to bats (Sedgeley and O'Donnell, 1999b). The number of cavities/tree was recorded and each cavity was classified as one of four cavity types (see below).

### Measuring structural characteristics of trees and cavities

We used five variables to characterise roost trees and potentially available trees: tree species; stem diameter (cm DBH); trunk height (m) (measured with a clinometer, Suunto, Helsinki, Finland); overall tree height (m); and number of cavities per tree.

No characteristics of available cavities, except for cavity type, were measured in this study (see below). We used 12 variables to characterise roost cavities. Seven external characteristics were measured: (1) the diameter of the trunk or branch containing the cavity

measured at cavity height (cm DCH); (2) the height of cavity from the ground (m); (3) the mean of eight horizontal distances at 45° intervals measured from the centre of the tree at cavity level to the nearest vegetation (m); (4) the vertical distance to the nearest vegetation immediately above and below the cavity (m); (5) the cross-sectional area of the entrance hole (height x width) (cm<sup>2</sup>); (6) the number of entrance holes into the cavity; and (7) the direction the entrance faced (aspect in 4 quadrants, NE, NW, SE, SW).

We used a torch bulb connected to a flexible piece of wire and a telescopic dentist's mirror to see inside the cavities. Dimensions were measured with a flexible metal tape measure. We measured four internal characteristics (Sedgeley and O'Donnell, 1999b): (1) the horizontal cross-sectional area of the cavity (distance between the entrance and the back wall of the cavity x distance between the side walls) (cm<sup>2</sup>); (2) cavity height (depth of cavity below entrance + height of cavity above entrance) (cm); (3) an estimate of cavity wall thickness (DCH minus distance between side walls divided by 2) (cm); and (4) cavity volume as a rectangular polyhedron based on multiplying together other internal dimensions (cm<sup>3</sup>). In addition, we classified each cavity according to type as either a knot-hole (small-medium sized well defined internal cavities probably formed by branch death), a split [large cavities with long (>30 cm) narrow entrances], a hollow (entrance holes opening into an open hollow tree trunk, probably formed as a result of stem/heart rot), or as a basal hollow (same definition as hollow, but opening out at ground level) [adapted from Sedgeley and O'Donnell (1999b)].

### Measuring roost temperature

To describe the microclimate inside communal roost cavities, we measured internal cavity temperature and compared it with external ambient temperature. To record temperature we used small temperature data loggers (Onset Stowaway XTI02®, range -39 to +122°C, accuracy (±0.5°C) with external probes (PB35-60) (Hastings Data Loggers, Port Macquarie, N.S.W., Australia). External ambient temperature data were collected continuously from a recording station central to the study area. The logger and probe were screened to shield them from direct sunlight and suspended below the canopy at 3 m above the ground (approximate average roost height). We measured temperature inside roosts by inserting temperature probes directly into unoccupied cavities and positioning them at the highest point (the place where bats most frequently roosted). The data logger took 100 evenly spaced samples per hour and recorded the mean of those samples on the hour over a 3-day period. Data were not collected from all cavities at the same time, but cavity and ambient data were collected

simultaneously.

Recording began at 1200 h and finished on the 3rd day at 1200 h. Data were averaged per hour and categorised into hourly intervals over each 24-h period: data collected between 1201 h and 1300 h were assigned to hour 13, etc. Hourly data were used to calculate variables that would illustrate pattern and variation in temperature for each 24-h period: maximum, minimum; range; mean rate of change per hour; time of day maximum temperature occurred; and length of time maximum temperature was maintained. These results were then averaged over the recording period to generate mean variables for a 24-h period which were then compared between roost and ambient sites (after Sedgeley, 2001).

### Statistical analysis

Initially, we used univariate statistics to test whether there were differences between characteristics of sites used by bats and those potentially available. Tree and cavity structural data, and data used to describe roosting behaviour were skewed with non-normal distributions (tested with the Wilks-Shapiro Statistic, *W*). Most variables could not be transformed successfully, and non-parametric Mann-Whitney *U*-tests and Kruskal Wallis one-way analysis of variance tests were used to compare samples.

Results for tree and cavity data are expressed as medians and interquartile ranges, and roosting behaviour and temperature data are expressed as means ± 1 S.D. Chi-squared and Fisher's Exact tests were used to test differences in frequency distributions between samples. To test whether bats either selected or avoided roosting habitat (habitat type, tree species, and cavity type) (i.e. exhibited non-random use), we calculated the *z*-statistic with Bonferroni adjusted 95% confidence intervals for each habitat use-availability ratio (Neu *et al.*, 1974; White and Garrott, 1990). When relative use (proportion of bat activity ± confidence intervals) of a particular habitat was significantly greater than expected when compared to availability, we considered the habitat to be selected (*P* < 0.05). When use was significantly less than expected we considered the habitat to be avoided, but if there was no significant difference between use and availability we termed the habitat to be used at random (Neu *et al.*, 1974; Manly *et al.*, 1993; Bradshaw *et al.*, 1995; Walsh and Harris, 1996).

Ambient and roost cavity temperature data at Hanging Rock were normally distributed and were compared using paired *t*-tests. Temperature data from Hanging Rock and from the Eglinton Valley (Sedgeley, 2001) were collected in different years. Therefore, patterns of temperature within cavities were compared between study areas, but variation in absolute temperature (maximum, minimum; range) were not.

We used logistic regression (SPSS 10.0 Software Products, Chicago, U.S.A., 1999) to determine which of the variables measured best discriminated between communal roost cavities used by bats at Hanging Rock and bats from the Eglinton Valley (Sedgeley, 2003). Logistic regression is particularly suitable for habitat association studies when habitat variables often have non-normal distributions, are categorical, and the sampling design is retrospective (Ramsey *et al.*, 1994; Manel *et al.*, 1999). Final selection of the model involved backward elimination of non-significant effects. Initially, we entered all variables into a model, and then at each step the variables were evaluated for entry and removal (e.g. Robb *et al.*, 1996; Brigham *et al.*, 1998). The procedure removed correlated variables. The score statistic was used for determining whether a variable should remain in a model ( $P < 0.05$ ), and the likelihood-ratio statistic was used to select variables for removal ( $P > 0.10$ ). Positive variable coefficients indicated that an increase in the value of a variable increased the probability of a cavity being a roost from Hanging Rock. A negative coefficient indicated that as the value of a variable increased, the probability of being a roost from Hanging Rock decreased. Likelihood-ratio tests were used to assess the contribution of individual variables to the model. Our assessment of goodness-of-fit of the final (best-fit) model was based on Hosmer and Lemeshow lack-of-fit test (Hosmer and Lemeshow, 1989) and classification accuracy (comparing predictions with observed outcomes, cut value = 0.50).

## Results

### Number of roosts located

We followed radio-tagged bats to a total of 94 roosts. Nineteen roosts (20.2%) were in crevices and holes in the Hanging Rock limestone escarpment, and 75 (79.8%) were in trees. No roosts were found in buildings despite their relative abundance. Excluding the town of Pleasant Point (Fig. 2), a minimum of 793 dwellings and farm buildings were scattered throughout the study area (counted from topographical map NZMS 260, J38).

### Roosting behaviour

Fifty-percent of all roosts found were communal, 42.5% were solitary, and 7.5% (all in rock) were unclassified. Communal roosts were occupied by bats (tagged and untagged) for an average of  $1.6 \pm 0.1$  days ( $n = 57$ , range = 1 to 6 days). Bats always left their roost site (to move on to a new site) simultaneously as a group. Solitary roosts were occupied for  $1.5 \pm 0.1$  days ( $n = 43$ , range = 1 to 5 days). There was no significant

difference in residence time between the two roost types ( $U = 749.5$ ,  $P = 0.536$ ). Most roosts (86.2%) were only used once during the 3-year study period by radio-tagged bats. Thirteen (13.8%) were used on more than one occasion. Four solitary roosts were each used twice, eight communal roosts were used twice, and one communal roost was used three times. The mean size of bat colonies was  $9.8 \pm 1.1$  bats ( $n = 65$  roost counts, range = 2 to 38).

We caught a total of 242 bats in harp-traps at 20 different tree roosts. The number of captures ranged from 2 to 38 individuals. We calculated the proportions of each sex and reproductive class for each roost. The mean composition of communal roosts was  $10.9 \pm 5.9\%$  breeding males,  $1.7 \pm 1.7\%$  non-breeding males,  $68.9 \pm 6.5\%$  breeding females,  $9.0 \pm 5.0\%$  non-breeding females, and  $9.4 \pm 4.1\%$  juveniles. Sixty-one percent of roosts that contained breeding females and young (described hereafter as maternity roosts) were located in non-native willow trees, with the remainder spread over six other tree species. Communal roosts found in crevices in Hanging Rock escarpment ( $n = 12$ ) were occupied outside the main breeding season (up to early pregnancy, and after lactation).

### Selection of roost sites

Many of the roosts in the Hanging Rock limestone escarpment were inaccessible. As a consequence no structural characteristics of these roosts were measured in this study (but see Griffiths, 1996). It was not possible to gain access to all roost cavities in trees (e.g. those located in dead limbs), therefore sample sizes for individual characteristics vary.

### Roosting habitat

Bat roosts were not distributed at random throughout the dominant land classes in the Hanging Rock area. Bonferroni analysis indicated that bats selected roost sites within three land classes: indigenous podocarp forest remnants; indigenous shrublands dominated by kanuka and cabbage trees; and mature introduced willows along river and stream banks. Bats appeared to use plantations of exotic trees at random, and roosted in indigenous trees within these plantations. Thirty-seven per cent of roosts were found in pastoral areas, but this land class was used significantly less than expected relative to its availability. All roosts found in the limestone were within the pastoral landclass. No roosts were found in exotic shrubland, urban areas or on open riverbeds (Table 1).

### Roost trees

The 348 available trees comprised 37 species, and bats roosted in nine of these species and dead trees. Cavity-bearing trees were rare in the landscape. Only 16% of

**Table 2.** Comparison of randomly available tree species and tree species used by communal and solitary roosting *Chalinolobus tuberculatus* at Hanging Rock. Available trees were sampled along 50 one km random transects throughout the study area. Results expressed as proportions, and selection of tree species is assessed using Bonferroni analysis and expressed as 95% Confidence Intervals (BCI).

Tree type	Proportions of each tree type available	Roost type	Proportion of roosts found in each tree type (with BCI)		Preference
Other species	0.267	Communal	0	–	Not used
		Solitary	0	–	Not used
Conifers <sup>1</sup>	0.241	Communal	0.071	(0–0.163)	Avoided
		Solitary	0.061	(0–0.158)	Avoided
<i>Salix fragilis</i>	0.210	Communal	0.500	(0.320–0.680)	Selected
		Solitary	0.151	(0.006–0.296)	Random
<i>Populus</i> spp. <sup>3</sup>	0.138	Communal	0.095	(0–0.200)	Random
		Solitary	0	–	Not used
<i>Cordyline australis</i> <sup>2</sup>	0.080	Communal	0.167	(0.033–0.301)	Random
		Solitary	0.333	(0.143–0.523)	Selected
<i>Kunzea ericoides</i> <sup>2</sup>	0.032	Communal	0.048	(0–0.125)	Random
		Solitary	0.212	(0.046–0.378)	Selected
<i>Quercus</i> spp.	0.017	Communal	0	–	Not used
		Solitary	0.030	(0–0.099)	Avoided
Dead trees	0.009	Communal	0.095	(0–0.200)	Random
		Solitary	0.212	(0.046–0.378)	Selected
<i>Acacia</i> spp.	0.006	Communal	0.023	(0–0.077)	Random
		Solitary	0	–	Not used

<sup>1</sup>*Cupressus macrocarpa*\*, *C. leylandii*, *Pinus radiata*\*, *Sequoia gigantea*, *Thuja plicata*

<sup>2</sup>Indigenous tree species

<sup>3</sup>*Populus alba*\*, *P. nigra*\*, *P. nigra* var. *italica*

\* Used as roost trees

randomly sampled trees contained cavities. Thirty-six percent of the total number of bat roosts were in indigenous tree species, a significantly higher proportion than was available (17%) (Fisher's Exact test,  $P < 0.001$ ). Bats were selective of individual trees, preferring to roost in cabbage trees, kanuka, willow and dead trees (85% of roosts), and avoiding conifers and oak trees (*Quercus* spp.). A higher proportion of communal roosts was found in willow than any other species, and 61% of maternity roosts were in willows. Several other tree species were used in proportions that were not significantly different to availability (Bonferroni analyses, Table 2). Communally and solitary roosting bats showed differential roost

selection, with bats occupying communal roosts only selecting willow trees (Table 2). Higher proportions of solitary roosts were found in cabbage trees and kanuka.

The structural characteristics of roost trees were also distinct from randomly sampled available trees (Table 3). Bats occupying communal roosts selected trees that had larger stem diameters and greater trunk height than trees used as solitary roosts and random trees (which did not differ from each other) (Kruskal-Wallis comparison of mean ranks,  $P < 0.05$ ). Communal and solitary roost trees had significantly more cavities/tree than random trees, but did not differ significantly from each other (Kruskal-Wallis comparison of mean ranks,  $P < 0.05$ ).

**Table 3.** Comparison of randomly available tree characteristics and characteristics of tree used by communal and solitary roosting *Chalinolobus tuberculatus* at Hanging Rock. Available trees were sampled along 50 one km random transects throughout the study area. Data are expressed as medians (med.) with inter-quartile ranges (IQ range). Comparisons were made using Kruskal-Wallis one-way analysis of variance tests.

Variable	Randomly available trees			Communal roosts			Solitary roosts			P
	n	med.	IQ range	n	med.	IQ range	n	med.	IQ range	
DBH (cm)	347	36.0	24.0–65.0	40	45.0	29.0–109.0	32	32.0	18.8–60.0	0.012
Trunk height (m)	340	2.0	1.4–4.0	34	5.8	2.5–10.0	24	2.0	1.7–3.9	<0.001
Tree height (m)	347	10.0	7.0–16.0	36	13.5	8.0–28.0	29	8.0	7.0–11.0	0.061
No. of cavities	332	0	0–0	32	2.0	1.3–4.8	23	3.0	1.0–5.0	<0.001

### Roost cavities

Communal bats selected roosts in longitudinal splits in trunks and main branches and avoided large open trunk-hollows. Solitary roosting bats showed no preference for roost cavity type (Table 4). An additional two roosts were found under loose bark, but the availability of loose bark was not quantified. No other variables were measured for available cavities in this study, so we do not know whether bats at Hanging Rock selected roost cavities with other distinctive characteristics. However, communal and solitary roost cavities were distinctive, with 6 of the 9 continuous

cavity variables measured differing between the two roost types (Table 5). Communal roosts had significantly larger stem diameters at cavity height (DCH), larger cavity entrances and internal dimensions, and significantly thicker cavity walls (Mann-Whitney *U*-tests,  $P < 0.05$ ) (Table 5). The aspect towards which roost entrances faced was evenly distributed for both communal ( $\chi^2 = 4.4$ , d.f. = 3,  $P = 0.218$ ) and solitary roosts ( $\chi^2 = 0.8$ , d.f. = 3,  $P = 0.849$ ), and there was no significant difference in the number of cavity entrances between communal and solitary roosts (Fisher's Exact test,  $P = 0.175$ ).

**Table 4.** Comparison of available cavity type and the type of cavity used by communal and solitary roosting *Chalinolobus tuberculatus* at Hanging Rock. Results expressed as proportions, and selection of cavity type assessed using Bonferroni analysis and expressed as 95% Confidence Intervals.

Cavity type	Proportions of each cavity type available	Roost type	Proportion of roosts found in each cavity type (with BCI)		Preference
Knot-hole	0.387	Communal	0.278	0.105–0.451	Random
		Solitary	0.500	0.272–0.728	Random
Split	0.200	Communal	0.583	0.392–0.774	Selected
		Solitary	0.384	0.163–0.605	Random
Hollow	0.253	Communal	0.111	0–0.232	Avoided
		Solitary	0.115	0–0.260	Random
Basal hollow	0.160	Communal	0.028	0–0.091	Avoided
		Solitary	0	-	Not used

**Table 5.** Differences in characteristics of cavities used by communally and solitarily roosting *Chalinolobus tuberculatus* at Hanging Rock. Data are expressed as medians and inter-quartile ranges, and comparisons are made using Mann-Whitney *U*-tests.

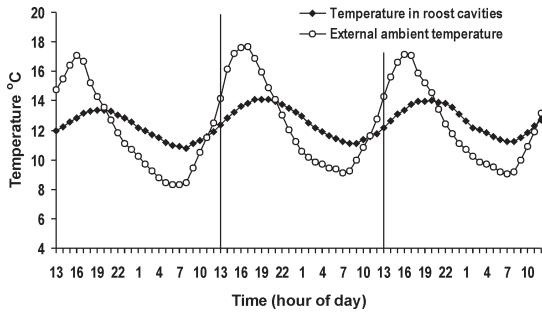
Variable	Communal roosts			Solitary roosts			<i>P</i>
	<i>n</i>	med.	IQ range	<i>n</i>	med.	IQ range	
DCH (cm)	35	36.0	18.0–60.0	24	16.5	12.8–25.0	<0.001
Height from ground (m)	36	4.0	2.5–5.9	26	3.7	2.7–6.1	0.819
Horizontal clutter (m)	24	5.0	1.9–6.5	17	4.9	1.8–129.1	0.596
Vertical clutter (m)	23	2.0	1.2–3.3	18	2.3	1.5–65.9	0.581
Entrance area (cm <sup>2</sup> )	31	144.0	60.0–301.0	24	43.9	18.5–89.5	0.001
Inside cross-sectional area (cm <sup>2</sup> )	27	88.0	45.0–168.0	18	39.0	23.0–57.0	<0.001
Internal cavity height (cm)	28	83.5	48.5–121.0	15	50.4	15.0–67.0	0.008
Volume (cm <sup>3</sup> )	27	12095.0	3544.5–19412.0	15	1209.6	300.0–4368.0	<0.001
Wall thickness (cm)	27	14.0	6.0–22.0	18	6.0	4.8–10.5	0.016

### Temperature inside roosts

We compared temperature inside 12 maternity roosts (measured during the lactation period) with external ambient temperature (described hereafter as ambient temperature). Overall, mean temperatures inside roost cavities did not fluctuate as greatly as ambient temperature over the 3-day sampling periods (Fig. 3). Mean temperature range inside roost cavities ( $3.8 \pm 0.7^\circ\text{C}$ ), was significantly less than ambient temperature range ( $9.3 \pm 1.2^\circ\text{C}$ ) ( $t = -5.2$ , d.f. = 11,  $P < 0.001$ ). Roost cavity maximum temperatures were significantly

cooler ( $3.3 \pm 0.9^\circ\text{C}$  cooler), and roost minimum temperatures were significantly warmer ( $2.2 \pm 0.4^\circ\text{C}$ ), than ambient temperatures (paired *t*-tests,  $P < 0.001$ ). Roost temperatures also changed at a slower rate per hour than ambient temperatures ( $t = 5.8$ , d.f. = 11,  $P < 0.001$ ). On average, the maximum temperature inside roosts was reached at 1800 ( $\pm 0.5$ ) h, a significant delay of  $1.8 \pm 0.6$  h from when ambient temperature peaked at 1600 ( $\pm 0.5$ ) h ( $t = -2.3$ , d.f. = 11,  $P = 0.043$ ). The maximum temperature in roosts was retained for significantly longer ( $4.3 \pm 1.4$  h) than ambient maximum





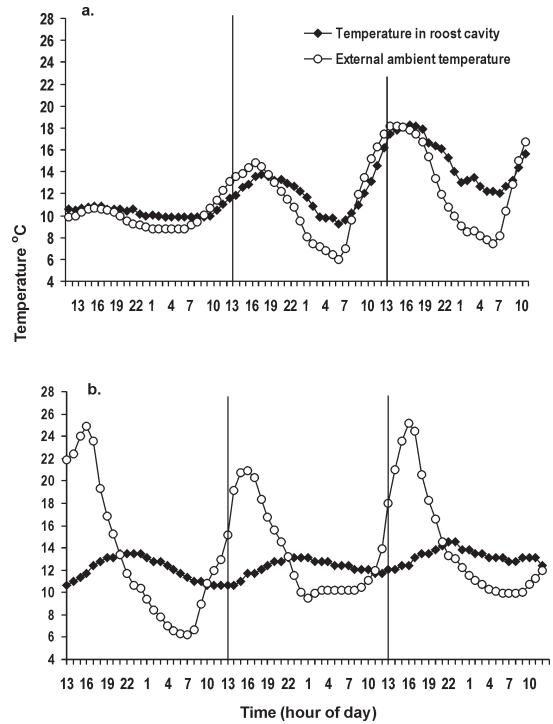
**Figure 3.** Average hourly temperatures recorded inside maternity roosts ( $n = 12$ ) used by lactating *Chalinolobus tuberculatus* at Hanging Rock compared with external ambient temperature over a 3-day period. Recording began at 1200 h and data points are shown in one hour increments, where 13 = 1201–1300 h, etc. For purposes of clarity error bars are not presented (SD of mean hourly temperature inside roosts = 1.65–4.06 °C, and external ambient = 1.28–6.70 °C).

temperature ( $1.0 \pm 0$  h) ( $t = -2.3$ , d.f. = 11,  $P < 0.001$ ). There was, however, considerable variation in degree of insulation among the 12 roosts. Temperatures inside seven of the roosts (6 in willows with large cavity entrances, and 1 in a small cabbage tree with a large entrance), fluctuated in a daily pattern similar to ambient temperature (e.g. Fig. 4a). In contrast, temperature fluctuations inside five roosts (3 in willows with small cavity entrances and 2 in non-willows), were relatively small compared with ambient conditions (e.g. Fig. 4b).

**Comparisons with *C. tuberculatus* in the Eglinton Valley**

*Modelling structural characteristics of cavities*

We entered six variables (DCH, height from ground, entrance area, inside cross-sectional area, internal height and wall-thickness) into a stepwise logistic regression analysis to examine which characteristics described most of the structural variation between communal roost cavities used by bats at Hanging Rock, and in the Eglinton Valley. Vegetation clutter was not included because differences in this variable between the two study areas was likely to be an incidental function of habitat type (i.e. all Eglinton Valley roosts were located within forest). The final (best-fit) model indicated three main variables explained most of the variation between Hanging Rock and Eglinton Valley bat roosts. As cavity entrance size increased and as internal cavity wall thickness and height of cavity from the ground decreased a cavity was more likely to be a communal roost from Hanging Rock (Table 6). This model correctly classified Hanging Rock roosts and Eglinton Valley roosts 96.3% and 95.8% of the time respectively,



**Figure 4.** Variability in thermal qualities (average hourly temperatures) of roost cavities used by lactating *Chalinolobus tuberculatus* at Hanging Rock. (a) Example of a less well insulated cavity that had a relatively large entrance, and was inside a small diameter cabbage tree (*Cordyline australis*). (b) Example of a relatively well insulated cavity that had a comparatively small entrance, and was inside a large diameter willow (*Salix fragilis*).

and the Hosmer and Lemeshow lack-of-fit test suggested the model fitted these data well ( $\chi^2 = 0.31$ , d.f. = 7,  $P = 1.000$ ).

*Roost temperature*

Temperature patterns inside roosts from the Eglinton Valley ( $n = 24$  maternity roost cavities) were very similar to those observed in roosts at Hanging Rock (e.g. roosts had smaller ranges and rates of temperature change than ambient conditions, and maximum roost temperature occurred later in the day and was held for several hours, Sedgely, 2001). However, compared with roosts from Hanging Rock, temperatures inside Eglinton Valley roosts changed at a slower rate per hour, had a greater time-lag between when ambient and roost temperature peaked, and their maximum temperature was maintained for significantly longer (two sample  $t$ -tests,  $P < 0.01$ ).

**Table 6.** Best fit model for logistic regression of cavities used as communal roosts by *Chalinolobus tuberculatus* at either Hanging Rock ( $n = 27$  roost cavities) or in the Eglinton Valley ( $n = 48$  roost cavities).

Variable	Coefficient	S.E.	Model log likelihood	Change in -2 log likelihood	d.f.	Significance of change ( $P$ -value)
Height from ground	-2.584	1.304	-39.068	66.627	1	0.000
Entrance area	0.003	0.003	-9.646	7.784	1	0.005
Wall-thickness	-0.281	0.164	-8.537	5.566	1	0.018

## Discussion

### Evidence for roost-site selection

During the summer months *C. tuberculatus* at Hanging Rock selected roosting habitats and roost trees with characteristics that were distinct from potentially available sites. The bats selected particular tree species within indigenous forest and shrubland remnants, and riparian zones. Communally roosting bats demonstrated a higher degree of selectivity by roosting in splits in some of the largest trees available, predominantly willows. In contrast, bats that roosted alone selected a wider range of tree species in which to roost, roost trees were of a similar size to available trees, and no preference was shown for roost cavity type. Although the availability of rock crevices was not measured, limestone bluffs were a common feature in the pastoral land class. We assume trees were the preferred roost sites of breeding bats because no maternity roosts were found in any other roost type during the main breeding season.

The selection of some of the largest trees available as roost sites by bats at Hanging Rock is similar to behaviour of bat species occupying unmodified forested habitats (Vanhof and Barclay, 1996; Menzel *et al.*, 1998; Rabe *et al.*, 1998; Sedgeley and O'Donnell, 1999a). Other studies have shown that bats inhabiting fragmented and highly modified landscapes also select roosts in the largest trees available (Law and Anderson, 2000; Lumsden *et al.*, 2002). Bats may use large trees simply because they are of a sufficient size and age to have developed cavities suitable for roosting. The number of cavities in a tree increases with stem diameter (Bennett *et al.*, 1994; Sedgeley and O'Donnell, 1999a). Trees with larger stem diameters also provide greater insulation to roosting bats, thereby reducing their thermoregulatory costs (Sluiter *et al.*, 1973; Maeda, 1974; Sedgeley, 2001; Wiebe, 2001).

*Chalinolobus tuberculatus* in the Eglinton Valley (Sedgeley and O'Donnell, 1999a) and other bat species selected particular tree species as roost sites (e.g. Lunney *et al.*, 1995; Vanhof and Barclay, 1996; Foster and Kurta, 1999). However, *C. tuberculatus* may not have discriminated between tree species *per se*, but

may have selected trees on the basis of their functional characteristics, i.e. their ability to develop suitable roost cavities. For example, *C. tuberculatus* in the Eglinton Valley selected roosts in red beech trees. This tree species is more likely to form cavities due to its susceptibility to decay and wood-boring beetles, and is better able to provide insulation due to its thick bark and larger stem diameter size than other available species (Sedgeley and O'Donnell, 1999a). Of the total 37 species of available trees sampled at Hanging Rock, 17 species had cavities, but bats used only 9 of these species and the majority of roosts was in willows. Cabbage trees and kanuka have relatively small stem diameters compared with willows, and solitary roost trees and cavities were significantly smaller than communal roosts in this study. It appears that willows are selected primarily as roost sites because they are one of the few tree species at Hanging Rock that develop cavities large enough for use by communally roosting bats.

### Implications of roost-site selection

Since bats do not build nests, and few species structurally modify their roosts, selection of a roost site can have a major influence on reproductive success and survival (Kunz, 1982). High quality roosts are generally higher from the ground allowing for easy detection of, and escape from, predators. They are close to available food and provide a thermal environment resulting in energetic benefits to the occupants [reviewed in Sedgeley (2001)]. We assume *C. tuberculatus* at Hanging Rock selected the best quality available cavities as roost sites. Communal and solitary cavities differed significantly from each other suggesting the bats did discriminate amongst available cavities, selecting roosts best suited to their social, reproductive or energetic requirements. Energy demands are high during pregnancy and lactation (Speakman and Racey, 1987; Kurta *et al.*, 1989). Consequently breeding females tend to use maternity roosts that have structural properties that allow them to cluster together and derive energetic benefits from behavioural thermoregulation [reviewed in Kunz (1982)]. A warm roost environment will promote

increased rates of gestation and post-natal growth (Racey, 1973; Racey and Swift, 1981; Hoying and Kunz, 1998). Selection of warm roost sites may be one of the most important mechanisms by which breeding females can reduce energy expenditure with little cost to reproductive success.

Despite these preferences, the maternity roosts at Hanging Rock do not appear to provide optimal roosting conditions. Ninety-seven percent of the indigenous forest cover has been cleared over the last *c.* 150 years at Hanging Rock (Fig. 1) and consequently cavity bearing trees are rare, and large-diameter, well-insulated trees are few. Productivity and survival in the Hanging Rock population was significantly lower than in the Eglinton Valley. Annual productivity at Hanging Rock averaged 0.24 young weaned/parous female. The probability of juveniles surviving to their first year averaged 0.23 (O'Donnell and Sedgeley, 2004). In contrast, annual productivity in the Eglinton Valley averaged 0.91 young weaned/parous female and survival to first year averaged 0.53 (O'Donnell, 2002). Both study areas have cold-temperate climates and are at similar altitudes, although the Eglinton Valley is wetter and slightly cooler. Annual rainfall reaches >5000 mm/yr in the upper valley and mean monthly temperatures vary from 5.1°C in July to 15.6°C in January (O'Donnell, 2002). We suggest that the difference in the thermal qualities of roosts at Hanging Rock and in the Eglinton Valley is an important factor explaining differences in productivity. Several other factors (and their interactions) may also contribute to the differing rates of productivity and survival observed in the two bat populations, and these are discussed below.

Although all maternity roost cavities used at Hanging Rock were relatively buffered from external ambient temperatures, a proportion of these roosts had comparatively less stable conditions and more closely followed ambient temperature than roosts in the Eglinton Valley (e.g. Fig. 4a). Our logistic regression model indicated that two structural characteristics that are likely to influence cavity insulation (thinner cavity walls and larger entrances) described a large proportion of the variation between roosts in the two study areas. Alternatively, the wood density of tree species used as roosts at Hanging Rock may be less than that of the beech trees in the Eglinton Valley. Wood density was not measured in this study. Roost cavities in the Eglinton Valley held maximum temperatures for longer (5.8 h) and mean temperature ranges (1.9°C) were smaller than roosts at Hanging Rock (Sedgeley, 2001). Both differences are likely to be significant biologically. Relatively small differences in average roost temperatures (0.5–1.2°C) can affect energy expenditure in roosting bats that remain active and homeothermic (Entwistle *et al.*, 1997; Sedgeley, 2001). *Chalinolobus*

*tuberculatus* could save 3.4–7.3% of their daily energy budget by selecting cavities with stable temperatures. Greater energy savings would occur at night and likely benefit nonvolant young (which are left alone for 30–60% of the night) more than adult females (Sedgeley, 2001).

It is also possible that groups of bats at Hanging Rock are less likely to modify the internal microclimates of their roosts compared with bats in the Eglinton Valley. Temperatures in this study were measured while roosts were unoccupied, but other studies have shown that the metabolic heat generated by roosting bats can increase temperatures inside occupied roosts by 5–10°C above that of unoccupied roosts (e.g. Burnett and August, 1981; Kunz, 1987; Kalcounis and Brigham, 1998). The average roosting group size at Hanging Rock (mean = 9.8 bats) was significantly smaller than roosting groups in the Eglinton Valley [mean = 34 bats, O'Donnell and Sedgeley (1999)], but their roost cavities were significantly larger. Therefore, roosting groups at Hanging Rock may be less able to increase roost temperatures by metabolic heat, and their roosting cavities, when occupied, are likely to be cooler.

Thermoregulatory patterns in bats vary among reproductive stages and individuals will select roosts to match their thermoregulatory strategy (e.g. Lausen and Barclay, 2002, 2003). *Chalinolobus tuberculatus* can also achieve significant energy savings by entering torpor (Webb 1998, 1999), and by roosting in cooler cavities to facilitate use of torpor (Audet and Fenton, 1988; Entwistle, 1994). Bats commonly use this strategy during unfavourable conditions (i.e. low food availability, poor weather conditions). Non-reproductive bats regularly use torpor, but it is used less frequently by breeding females (Audet and Fenton, 1988; Hamilton and Barclay, 1994; Grinevitch *et al.*, 1995) because its benefits can be outweighed by costs to reproduction. Pregnant and post-lactating bats use torpor, and lactating bats will use shallow torpor, but the use of deep and prolonged torpor is limited in lactating bats (Lausen and Barclay, 2003). The cost:benefit ratio of torpor can be particularly high during lactation and can result in decreased milk production and juvenile growth rates (Racey, 1982; Kunz, 1987; Wilde *et al.*, 1995), which in turn can have implications for both juvenile and adult over-winter survival (Tuttle and Stevenson, 1982; Zahn, 1999). Therefore, lactating females in particular, will tend to select roosts with warm conditions that allow them to reduce energy expenditure while remaining active and homeothermic (e.g. Kerth *et al.*, 2001), or well-insulated roosts that retain warmth for nonvolant young that remain in the roost at night, and are cool enough in the day to allow shallow torpor, which may be important to compensate for the costs of lactation (e.g. Lausen and Barclay, 2002, 2003).

Temperatures in this study were measured inside maternity roosts during the lactation period. Therefore, it seems strange that the lactating females moved between sites of differing thermal qualities rather than stay in those that were warmer and better insulated. However, the temperature data gathered at Hanging Rock was from a relatively small subset of the total number of maternity roosts used. Therefore, we do not know what proportion of time lactating bats spent in less-insulated roosts. Neither do we know how individual breeding success varied. Limited by the findings of the present study, we can only infer that quality of roost microclimate may be a factor influencing reproductive success. The relationship between microclimate quality and reproductive success could be tested by comparing an index of maternity cavity quality (derived from temperature and structural components) with measures of individual fitness and the time spent in well-insulated roosts versus poorly-insulated roosts.

Bats at Hanging Rock only resided in roosts for an average of one day. This appears non-adaptive if optimal roosts are rare. However, extreme roost-site lability is a characteristic of tree-cavity roosting bats throughout temperate zones, including the Eglinton Valley (e.g. Vohnhof and Barclay, 1996; O'Donnell and Sedgely, 1999). Hypotheses explaining lability include minimizing commuting distances to foraging areas, and avoiding parasite build-up, predators or unfavourable changes in microclimate or structural conditions in a roost (Lewis, 1995). Despite frequent shifting, temperate bats are highly selective in choice of roosting cavity and frequent shifting appears normal in bats that are not forced into regular or continual use of caves and buildings. Bats in the Eglinton Valley moved frequently despite occupying individual trees that could provide roosting sites for hundreds of years (O'Donnell and Sedgely, 1999). Because they switch roosts often, social interdependence would increase the probability that clusters of bats would be large enough on any one day to provide thermal benefit and individuals could improve the reproductive success of other relatives within the group (O'Donnell, 2000b; O'Donnell and Sedgely, 2004). Despite bats moving frequently and roosting in a large number of trees it is likely that maternity roosts are used regularly. Although only 13% were reused during the present study, this was likely an underestimate of real use because transmitters remained attached for short periods (<10 days) and only 1–4 bats were tracked at any one time. In a much longer running study in the Eglinton Valley, we have found that bats return to maternity roosts on a regular cycle (O'Donnell and Sedgely, 2004).

Other factors may explain differences in fitness between the Hanging Rock and Eglinton Valley *C. tuberculatus* populations. These include variation in

pressure from introduced predators or catastrophic events, effects of isolation influencing levels of genetic diversity, quality of winter roost sites, and quality of foraging habitat.

Bat roosts at Hanging Rock were close to the ground and frequently had large entrances, characteristics likely to increase the vulnerability of bats to terrestrial predators. For example, possums were recorded visiting maternity roosts on six occasions at Hanging Rock [ $n = 8$  video-nights (C. O'Donnell, *unpubl.*)] and records of cat-killed bats are common in the study area (Daniel and Williams, 1981; Department of Conservation, unpublished records). Although relative predation risk between Hanging Rock and the Eglinton Valley has not been quantified, predators are also abundant in the Eglinton Valley. There appears to be a high risk of predation from introduced mammals at both sites. Stoats (*Mustela erminea*) and rats (*Rattus* spp.) periodically reach plague proportions in the Eglinton Valley and prey on both cavity-breeding forest birds and bats in significant numbers (O'Donnell *et al.*, 1996; Dilks *et al.*, 2003; Pryde, 2003). These predators are not limited to preying upon animals in cavities low to the ground.

Reliance on willows for roost sites may increase the risk from catastrophic events such as tree-fall. Willows are very fast-growing and reach maturity and a large size at a relatively young age. At Hanging Rock, willows seem to reach early senescence; many large trees are full of hollows and splits (which are necessary for roost formation), but limbs commonly fall off and trees fall over [ $n = 8$  during the study (C. O'Donnell, *unpubl.*)]. Landowners frequently 'tidy-up' old willows removing rotten and cracked branches, and large numbers of willows are routinely chopped down for firewood. During this study, four maternity roosts were chopped down before the landowner was alerted, and there is an earlier record of a bat found alive in a pile of firewood within the study area (Daniel and Williams, 1981). The Eglinton Valley lies within Fiordland National Park, consequently roost trees are protected by law from these latter activities.

Growth rates and survival in bats have been shown to be positively correlated with increased heterozygosity (Rossiter, 2000). The *C. tuberculatus* population at Hanging Rock was once larger, but has been reduced in size by loss of habitat and isolated by fragmentation (O'Donnell, 2000c), with inbreeding a likely consequence. Studies suggest loss of genetic variation can be rapid in populations of 50–100 individuals with consequent increases in inbreeding, and decreases in heterozygosity, fecundity, growth, survival, and resistance to disease (Frankel and Soulé, 1981; Gilpin and Soulé, 1986; Lacey, 1997). The larger and less isolated Eglinton Valley population (O'Donnell, 2000b) has greater potential for gene flow.

Differential survival of bats may also be related to food availability. However, foraging habitat appears to be of a higher quality at Hanging Rock, where survival is lower. During the summer months, bats in the Eglinton Valley foraged for most of the night and food appeared to be limited (O'Donnell, 2000a), whereas at Hanging Rock bats typically foraged for only a few hours each night (Griffiths, 1996; C. O'Donnell, *unpubl.*). Additionally, bats at Hanging Rock continued to be active later in the season than in the Eglinton Valley (Griffiths, 1996; O'Donnell, 2000a). These results suggest that insect abundance may be higher in fragmented habitats, or insects are more active in the slightly warmer, drier climate of Hanging Rock.

Bats at Hanging Rock may also face threats at their winter roost sites. Crevices in the limestone escarpment are used outside the breeding season and during winter (Griffiths, 1996). However, while such roost sites may be relatively abundant, Griffiths (1996) noted that bats were subject to regular disturbance from rock climbers, and competition from starlings (*Sturnus vulgaris*). Repeated disturbance of bats during hibernation can deplete fat reserves and result in increased rates of over-winter mortality (Speakman *et al.*, 1991; Thomas, 1995). Abandoned starling nests may prevent bats from using the crevices. No winter roost sites have been found in the Eglinton Valley.

### Conservation recommendations

Evidence points to a steady decline in *C. tuberculatus* populations since at least the arrival of Europeans in New Zealand. Since the mid-1800s there has been a marked reduction in this bat's range and abundance. Preliminary monitoring since 1990 indicates *C. tuberculatus* is now rare or absent at many sites where formerly it was common (O'Donnell, 2000c). Dwyer (1962) concluded that the decrease in distribution of *C. tuberculatus* was correlated with the removal of indigenous forest and the failure of bats to survive in open country and urban areas. *Chalinolobus tuberculatus* has persisted at Hanging Rock since at least the 1930s (Daniel and Williams, 1981, 1984). The indigenous forest remnants and willow-dominated riparian zones in the study area provide valuable foraging habitat for bats (Griffiths, 1996; C. O'Donnell, *unpubl.*), and together with the limestone escarpments, provide the most important roosting sites in the highly modified landscape. Unlike most tree species in the study area, willows readily develop cavities and provide one of the most abundant sources of roost cavities. Unfortunately many of these roost cavities appear to be of low quality, exposing occupants to relatively unstable microclimates and to a higher risk of threats such as predation. If maternity groups are forced into long-term use of lower quality roost sites, negative

effects on growth, productivity and survival will accrue, and eventually affect population viability adversely (Brigham and Fenton, 1986; Richter *et al.*, 1993; Zahn, 1999).

Direct conservation management may mitigate some of the negative effects of deterioration of roosting habitat and loss of roost quality due to human influences. We recommend six conservation measures to enhance the fitness of bat populations at Hanging Rock.

(1) Protection of existing roost sites. A high proportion of roosts are located on private land; roost sites need to be clearly identified and land owners encouraged to conserve roost trees and roosting habitat. It is important to acknowledge the importance of introduced willow trees as bat roosts. Willows are often regarded as weeds or pests.

(2) Enhancement of existing roosts. The insulating properties of existing roost sites at Hanging Rock may be improved by some form of exterior cladding, such as rubber. Restoration of the physical structure and microclimate of roosts has been successful in increasing the numbers and fitness of bats that breed and hibernate in caves (Richter *et al.*, 1993; Baudinette *et al.*, 1994). For example, raising the temperature inside a maternity roost of greater horseshoe bats (*Rhinolophus ferrumequinum*) resulted in significant increases in juvenile female growth rates and survival (R. D. Ransome, University of Bristol, Bristol, U.K. *unpubl.*).

(3) Provision of high quality artificial roosts in indigenous remnants and riparian areas. Kakahu Bush has good potential for regeneration, as both totara and matai regenerate strongly (J. Talbot, Trustee, South Canterbury Conservation Trust, Pleasant Point, N.Z., *pers. comm.*). Solitary bats already roost in kanuka shrubland in the study area, and the addition of artificial roost boxes would provide communally roosting bats with roost sites while larger cavities develop. Addition of well-insulated roost boxes into riparian areas may improve the quality of roosting habitat. Trials should be undertaken to determine which box designs (and positioning of them) are best able to provide appropriate microclimates and protection from predators and competitors (e.g. Calder *et al.*, 1983; McComb and Noble, 1981; Kerth *et al.*, 2001).

(4) Predator control in roosting habitat to alleviate the threat of possums and feral cats preying on bats.

(5) Bat advocacy. Information on bats, and on bat conservation, should be disseminated among local landowners, landcare groups, and statutory bodies.

(6) Replanting of vegetation to provide roosting habitat to sustain bat populations in the future. Regeneration is currently poor because of grazing throughout the study area. This means trees are not being replaced as they grow old and fall over. Although willows, cabbage trees or kanuka could provide a short-term solution to this problem they are relatively

short lived and are not guaranteed to develop optimum cavities suitable for roosts for long periods of time. Replanting should focus on indigenous tree species that provide good insulation and are long-lived.

Several of these recommendations are being considered or are taking place. The South Canterbury branch of the Royal Forest and Bird Protection Society has commenced a roost box scheme trailing 100 boxes of four different designs at Kakahu Bush. Local landowners have been sent information outlining the importance of trees to bats, and two fact sheets entitled 'Conserving long-tailed bat in South Canterbury' and 'Protecting old-age trees for New Zealand bats' are available on the Department of Conservation web site. The Department of Conservation and Environment Canterbury are also planning a programme of predator control in roosting areas. An important challenge for future researchers will be to assess the response of the bat population to these conservation measures testing, for example, whether fitness can be improved by enhancing roost cavity quality.

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