

Roost site selection and roosting behaviour in lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in *Nothofagus* forest, Fiordland

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Abstract I studied the roosting ecology of the lesser short-tailed bat (*Mystacina tuberculata*) during the summer months of 1997–2000 in lowland *Nothofagus* rainforest, Fiordland, New Zealand. Structural characteristics of communal day-roost trees and cavities were compared with those of randomly available trees and cavities, and those used by a sympatric population of long-tailed bats (*Chalinolobus tuberculatus*). I radio-tracked 29 *M. tuberculata* to 20 communal roost cavities located in 16 trees. Twelve of 21 characteristics measured differed significantly between roost and random sites. *M. tuberculata* selected roosts in more open parts of the forest, in some of the largest red beech (*Nothofagus fusca*) trees and cavities available. Characteristics of trees used by the two bat species were similar. Both species roosted in large diameter, old age red beech. However, 11 of the 12 roost cavity characteristics varied significantly between bat species. Roost cavities used by *M. tuberculata* were significantly lower to the ground, had more entrances, and had larger entrance and internal dimensions than *C. tuberculatus* roosts. Nevertheless, roosts of both species were well

insulated and exhibited stable internal temperatures. *M. tuberculata* roosting groups were dominated by females and young, and group size averaged 310 ± 88.1 bats ($n = 40$). Roosts were occupied for an average of 5.6 ± 6.9 days ($n = 23$). Group size was significantly larger than in *C. tuberculatus*, and roost residency time significantly longer. Differences in roost use and roosting behaviour between the two species should be considered when undertaking conservation management actions such as identifying trees for retention through logging cycles, or designating reserves.

Keywords bats; *Mystacina tuberculata*; *Chalinolobus tuberculatus*; tree roosting; roost-site selection; *Nothofagus*; temperate rainforest; New Zealand; conservation

INTRODUCTION

Future logging of native forests in New Zealand is subject to the Forest Amendment Act (1993) and the Resource Management Act (1991). These acts state that logging must be ecologically sustainable and avoid, remedy or mitigate, adverse affects on forest ecosystems. Past methods of logging in New Zealand have been detrimental to wildlife (O'Donnell 1991) and there is debate on whether new logging techniques can sustain ecosystem processes and wildlife (e.g., Efford 1998). The most effective way to predict whether logging will be detrimental to wildlife is to compare proposed tree harvesting regimes, e.g., sizes and ages of trees and length of harvesting cycles, with the specific requirements of wildlife.

Mystacina tuberculata and *Chalinolobus tuberculatus* comprise New Zealand's extant bat fauna, and are closely associated with indigenous forest (Daniel 1990). *M. tuberculata* and *C. tuberculatus* are the only native terrestrial mammals in New Zealand, 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). Both species of bat depend almost exclusively on trees as roost sites, and *M. tuberculata* forages extensively within the forest interior (Lloyd 2001; O'Donnell 2001).

Information on roost site preferences and roosting behaviour of bats will improve our understanding of how changes in land management practices might affect bat roosting habitat, and will aid in the formulation of conservation measures. Recently published research on *C. tuberculatus* focuses on roosting ecology in *Nothofagus* forest in Fiordland National Park. Bats roosted in small aggregations in well insulated knot-hole cavities within large red beech (*Nothofagus fusca*) trees that had distinctive structural and microclimatic characteristics relative to those available (O'Donnell & Sedgely 1999; Sedgely & O'Donnell 1999a,b). I have previously hypothesised that the roost characteristics *C. tuberculatus* selected would have implications for their breeding success and energy conservation (Sedgely 2001a). There is little published work of comparative detail describing roosting ecology and roost requirements of *M. tuberculata*, and none examining roost-site selection. *M. tuberculata* roosts in large hollows in trees, aggregating in larger groups than *C. tuberculatus* (numbering 100s and 1000s; O'Donnell et al. 1999; Lloyd 2001; Sedgely 2001b).

Differences have been found in roosting habitat, roost-site structure, microclimate, and roosting behaviour among sympatric bat species (e.g., Vonhof & Barclay 1996; Zahn & Henatsch 1998; Foster & Kurta 1999; Lumsden et al. 2002). Partitioning of roosting space has been observed in different bat species occupying the same roost (Swift & Racey 1983). Since morphology, foraging, and roosting behaviour of *M. tuberculata* and *C. tuberculatus* are distinctive (Lloyd 2001; O'Donnell 2001), I expected to find partitioning in roosting habitat, and to find differences in the structural characteristics of the roosts used by the two species.

In 1997 a population of *M. tuberculata* was discovered in the Eglinton Valley, Fiordland National Park, one of the few sites known to support large sympatric populations of both New Zealand bat species (O'Donnell et al. 1999). This provided a unique opportunity to compare the roosting ecology of New Zealand bats in unmodified *Nothofagus* forest. In this study I extend the preliminary data collected by O'Donnell et al. (1999) and aim to: (1) describe the structural and microclimatic characteristics of *M. tuberculata* roost sites; (2) test whether *M. tuberculata* selects roost sites with

distinctive characteristics compared with available sites; (3) describe the roosting behaviour of *M. tuberculata*; (4) compare roost use and roosting behaviour between *M. tuberculata* and *C. tuberculatus* to check for habitat partitioning; and (5) discuss the implications of roost selection for the conservation of bats.

MATERIALS AND METHODS

Study area

The study was conducted in the lower Eglinton Valley, Fiordland National Park. The valley is of glacial origin and has steep sides, a flat floor 0.5–2 km wide (c. 250–550 m above sea level), and an active shingle riverbed. Tussock grasslands dominated by *Festuca rubra* and *Anthoxanthum odoratum* and small patches of *Discaria toumatou* and *Corokia cotoneaster* shrubland cover much of the valley floor. *Nothofagus* forest covers gentle glacial terraces and outwash fans on the lower hill-slopes and then rises steeply to the timberline at 1000–1200 m a.s.l.

Red beech (*N. fusca*) and silver beech (*N. menziesii*) dominate the forest on the valley floor. Forest composition varies, ranging from pure stands of silver beech c. 20 m tall along the forest margin to tall stands of red beech up to c. 60 m tall farther into the forest. Mountain beech (*N. solandri* var. *cliffortioides*) occasionally contributes to the canopy at low altitudes, and becomes more common with increasing altitude. Below canopy the forest is generally open with few understorey plants and a ground cover of mosses. The most common understorey plants are mountain toatoa (*Phyllocladus aspleniifolius* var. *alpinus*), broadleaf (*Griselinia littoralis*), and *Coprosma* spp. The main roosting area for *Mystacina tuberculata* is situated at Knobs Flat. Mean annual rainfall averages 2300 mm per year at Knobs Flat, but increases markedly in a gradient to >5000 mm farther up the valley. Mean maximum daily temperatures are warmest in late summer (February, 14.7°C) and coldest in midwinter (July, 3.3°C) (Works Civil Construction, Te Anau, unpubl. data).

Capture of bats and location of roost trees

Roosts were found by following bats fitted with radio-transmitters (BD2A 0.7 g transmitters, Holohil Systems, Carp, Ontario, Canada). Bats were caught in mist nets set inside the forest. I radio-tracked 29

M. tuberculata (referred to hereafter as *Mystacina*; six adult males, 16 adult females, three juvenile males, and four juvenile females), four in 1997, 19 in 1998, four in 1999, and two in 2000. I attached transmitters between the scapulae using a latex-based contact adhesive (Ados F2, Ados Chemical Company, Auckland, New Zealand) after the fur had been partially trimmed with scissors. Transmitters represented an average of $4.7 \pm 0.7\%$ SD of the bats' body mass (range = 3.9–6.2%), a mean value below 5% of body mass recommended by Aldridge & Brigham (1988). I followed bats as long as transmitters were thought to be functioning or until they fell off. I located roost sites during the day by tracking using a TR4 receiver (Telonics, Arizona, USA) and 3-element hand-held Yagi antennae (Sirtrack, Havelock North, New Zealand). I generally identified roost cavities by climbing the tree and using the radio-receiver at close range. Occasionally cavities occupied by large groups of bats were identified by sounds of bats squeaking inside.

Assessing roost site selection

I examined roost site selection at the tree and cavity level, by comparing characteristics of roosts with those of random trees and cavities. Sampling of random trees and cavities was limited to those that were considered to be actually available to bats ("bat-available"). I sampled trees only if they were of sufficient size and age to contain cavities (>20 cm stem diameter, Sedgeley & O'Donnell 1999a). I considered cavities were available to bats if entrance and internal dimensions were sufficient for several bats to enter and find shelter. At least part of the cavity interior needed to be dry, to protect a group of bats from the elements.

Random trees were sampled throughout the roosting area using the point-centred quarter method (Causton 1988). This technique is particularly suitable for surveying trees and was used in previous studies of *C. tuberculatus* (referred to hereafter as *Chalinolobus*) in the Eglington Valley (Sedgeley & O'Donnell 1999a). I established 30 sampling points (point-centres) at random directions and distances from line transects through the main *Mystacina* roosting area. Four quadrants around each point-centre were marked and the nearest bat-available tree in each quadrant located and measured. This resulted in a sample of 120 random trees. I sampled random cavities along a transect line that ran through the roosting area. The transect was tagged every 100 m and I located the nearest bat-available tree to each

tag that had cavities. Every available cavity accessible by climbing was measured. If a tree had multiple cavities, only one cavity (chosen randomly), was included.

To assess whether the roosting habitat of *Mystacina* differed structurally from other parts of the forest, I compared "random plots" (derived from the point-centred quarter method above), with 15 "roost plots" which yielded 60 trees. Roost plots were sampled using roost trees as point centres rather than random points.

Measuring structural characteristics of forest, trees, and cavities

I used three variables to describe the structural characteristics of the forest stand; stem density/ha, composition of tree species, and canopy cover. Stem density/ha was calculated by measuring the distances to the nearest four bat-available trees around either the point-centres or the roost trees and averaged to get a stem density/ha/plot (Causton 1988). Tree species were recorded and frequency of occurrence over the total number of plots calculated. Canopy cover was estimated to the nearest 5% from the base of each tree (after Sedgeley & O'Donnell 1999a) and then averaged to give canopy cover per plot.

Six variables were used to characterise every roost tree and random tree identified: (1) tree species; (2) stem diameter at breast height (cm, DBH); (3) trunk height (m); (4) overall tree height(m); (5) canopy closure (%); and (6) number of cavities per tree. In addition, I measured the distance of each roost tree from forest-grassland edge (m) (after Sedgeley & O'Donnell 1999a).

Twelve variables were used to characterise roost and random cavities. Six external characteristics were measured: (1) the diameter of the trunk or branch containing the cavity at cavity height (cm DCH); (2) the height of the cavity above the ground (m, measured with a clinometer, Suunto, Helsinki, Finland); (3) the horizontal distance to the nearest vegetation at eight 45° intervals measured from the centre of the tree at cavity level (m, horizontal vegetation clutter); (4) the vertical distance to the nearest vegetation immediately above and immediately below the cavity (m, vertical vegetation clutter); (5) the cross-sectional area of the entrance hole (height \times width, cm²); and (6) the number of entrance holes into the cavity. A torch bulb connected to a flexible piece of wire and a telescopic dentist's mirror was used to see inside the cavities. Dimensions were measured with a flexible

metal tape-measure. Six internal characteristics were measured: (1) the horizontal cross-sectional area of the cavity (cm²); (2) cavity height (cm); (3) cavity depth (cm); (4) cavity volume as a rectangular polyhedron, calculated by multiplying together other internal dimensions (cm³); (5) an estimate of cavity wall thickness (cm) (DCH minus internal cavity width divided by 2); and (6) cavity type. Each cavity was classified as a knot-hole, split, trunk hollow or basal hollow (after Sedgely & O'Donnell 1999b).

Measuring roost temperature

I described microclimate inside communal roost cavities and compared cavity temperature with external ambient temperature (described hereafter as ambient temperature). I 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, NSW, Australia) to record temperature. A recording station was established within the forest, central to the main *Mystacina* roosting area to record ambient temperature continuously throughout the study. The logger and probe were screened to shield them from direct sunlight and suspended below the canopy 9 m above the ground (average roost height, O'Donnell et al. 1999). Temperature inside roosts was measured by inserting probes directly into unoccupied cavities at the highest point (the place where bats most frequently roosted). Temperature was recorded once every 5 min over 10, 5-day periods in January and February. Data were not collected from all cavities at the same time, but cavity and ambient data were collected simultaneously.

Temperature recording began at 1200 h and finished on the 5th day at 1200 h. Data were averaged per hour and categorised into hourly intervals over each 24-h period; data collected between 1201–1300 h were assigned to hour-13 etc. I used hourly data to calculate parameters to 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 roosts and the ambient site (after Sedgely 2001a). Temperature was measured inside unoccupied roost cavities after bats had vacated their roosts and moved to a new site to avoid the risk of disturbing the bats.

Describing roosting behaviour

Size and composition of roosting groups, roost residency times, and levels of roost reuse were used as measures of roosting behaviour. I counted bats as they emerged from roosts using an infra-red camera and video recorder. A wide-angle, buttonhole lens video camera (K. R. & J. A. Eccles, Upper Moutere, New Zealand), surrounded by 900 nm infra-red light emitting diodes, was mounted on a bracket outside roost cavity entrances. I recorded numbers of bats and traffic rates into and out of the roost cavities using a Panasonic AG-1070DC time-lapse video recorder (Matsushita Electric, Japan). I reviewed the tapes at slow speed to obtain accurate counts. I checked the locations of radio-tagged bats each day to assess how long roosts were occupied. If radio-tagged bats left a roost, monitoring would continue at the roost until all untagged bats had vacated.

I estimated the composition of groups of bats from five *Mystacina* roost trees by capturing samples of bats as they emerged from roosts after dusk. Harp-traps (4.2 m², Faunatech, Melbourne, Victoria, Australia) were positioned directly outside the roost cavities (Sedgely & O'Donnell 1996). I recorded age, sex, and reproductive status of all bats caught. Breeding females were defined as either 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). Young-of-the-year were identified by their unfused phalangeal epiphyses, and classified as juveniles. I could not determine the reproductive status of adult male *Mystacina*.

Data analysis

The majority of data describing *Mystacina* roosts and roosting behaviour was collected during the summer months of 1998–2000. The longest sampling period was in 1998 when the bats were studied for 3 consecutive months (January–March). The duration of each sampling period in 1999 and 2000 was 3 weeks (January–February). In addition, I include data collected in 1997 by O'Donnell et al. (1999). Thus, results presented in this paper are derived from data collected over four unequal sampling periods during the summer months of 1997–2000.

Initially, I used univariate statistics to characterise roosts relative to the attributes of bat-available trees and cavities. Some parameters were skewed with

non-normal distributions (tested with Wilks-Shapiro Statistic, W). Variables with non-normal data were transformed either by log or by $\log(x + 1)$ (Fowler & Cohen 1992). Where variables could not be transformed successfully, they were compared using non-parametric Mann Whitney U -tests. The remainder of comparisons were made with two-sample t -tests, and temperature data were compared using paired t -tests. Results are expressed as means ± 1 SD. Chi-square tests were used to test for differences in frequency distributions between samples. To examine differences in the frequency of tree species between roost and random plots the z -statistic with Bonferroni adjusted 95% confidence intervals was calculated for each tree species (Neu et al. 1974; White & Garrott 1990). When relative use of a particular tree species was significantly greater than expected, compared with availability, the species was considered to be selected ($P < 0.05$). When use was significantly less than expected the species was termed as avoided, but if there was no significant difference between use and availability it was considered to be used at random.

Logistic regression (SPSS 10.0 Software Products, Chicago, USA, 1999) was used to determine which of the significantly different variables best discriminated between roost and bat-available sites, and between *Mystacina* and *Chalinolobus* roosts. I used data describing roost trees and roost cavities of *Chalinolobus* from Sedgeley & O'Donnell (1999a,b). 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 models involved backward elimination of non-significant effects.

Initially all variables were entered into the models, then at each step variables were evaluated for entry and removal. The score statistic was used for determining whether a variable should remain in a model (if $P < 0.05$), and the likelihood-ratio statistic was used to select variables for removal (if $P > 0.10$). Wald's chi-square statistics were used to assess the contributions of individual variables to the models. Positive variable coefficients indicated that an increase in the value of a variable increased the probability of a tree or a cavity being a *Mystacina* roost. A negative coefficient indicated that, as the value of a variable increased, the probability of the tree or cavity being a *Mystacina* roost decreased. Assessment of goodness-of-fit or model performance was based on a Hosmer Lemeshow

lack-of-fit test and classification accuracy (comparing predictions with observed outcomes, cut value = 0.50) (Hosmer & Lemeshow 1989). Tree and cavity data were analysed in separate logistic regression analyses. Random tree and random cavity data from the *Mystacina* roosting area were derived from two different samples, and when both tree and cavity data were entered into a model comparing *Mystacina* and *Chalinolobus* roosts, the model became overfitted.

Therefore, I used four models that compared characteristics of: (1) *Mystacina* roost trees with random trees; (2) *Mystacina* roost cavities with random cavities; (3) *Mystacina* roost trees with *Chalinolobus* roost trees; and (4) *Mystacina* roost cavities with *Chalinolobus* roost cavities. Sample sizes among the various models vary because the logistic regression procedure drops cases from the model (listwise deletion) if any values within a case are missing.

RESULTS

Radio-tagged *Mystacina* were followed to only 29 roost cavities in 25 trees despite monitoring for 188 bat-days (mean = 6.2 ± 3.2 days/bat). Of these roosts, 20 roost cavities were occupied by aggregations of bats (described hereafter as communal roosts) in 16 trees. Four of the 16 roost trees contained multiple roost cavities (two trees had two roost cavities, and two had three roost cavities). None of these cavities were interconnected, and all had separate entrances. Thus, I consider these cavities to be distinctive enough to function as independent roosts, and treat them as such in subsequent analyses. Inaccessibility of some of the roost sites made it impossible to measure all characteristics, therefore sample sizes for individual tree and cavity characteristics vary.

Radio-tagged bats also roosted solitarily in nine roost trees, but only three of these cavities were located and measured. Two radio-tagged bats appeared to roost beneath bark. Because sample sizes are so small, these solitary roosts are not discussed further.

Selection of communal roost sites by *Mystacina*

Mystacina in the Eglinton Valley selected roost site characteristics at forest stand, tree, and cavity levels. Univariate statistical tests indicated that *Mystacina* were most selective at the forest stand and tree level, with all of the nine roost site characteristics examined differing from random sites. In contrast, only three

of the 12 cavity variables measured differed between roost and random cavities (Tables 1 and 2).

Forest structure around roosts

The composition of tree species (frequency of occurrence) differed between plots around roosts and random points (Table 1). *Mystacina* selected roosts in forest stands that had a significantly higher proportion of red beech, and avoided stands containing silver beech and other species. Dead trees occurred at similar frequencies on roost and random plots (Table 1). *Mystacina* selected roosts in forest with a relatively open structure. Mean stem density and canopy closure were significantly less on roost plots compared with random plots (Table 2).

Roost trees

Ninety-four percent of communal roosts were in red beech trees, a significantly higher proportion than available (Table 1). Mean stem diameter, trunk height and overall tree height of roost trees was significantly greater than random trees (Table 2) indicating *Mystacina* selected roosts in the largest trees in the forest. Roost trees had significantly less canopy closure than random trees and more cavities (Table 2). Eighteen percent of roost trees had one cavity, and the remainder had multiple cavities. In contrast, 63% of random trees had no cavities. All roost trees were located in the forest interior at a mean distance from the forest-grassland edge of 522.6 ± 481.7 m (range 150–1500 m).

Table 1 Characteristics (categorical variables) of forest stand (tree species composition), trees, and cavities used by *Mystacina tuberculata* compared with random sites. Analysis of forest stand structure compares composition of tree species from 15 plots around roost trees ($n = 60$ trees) with trees from 30 random plots ($n = 120$ trees). Analysis of tree characteristics compares 16 roost trees with 120 random trees, and analysis of cavity characteristics compares 20 roost cavities with 39 random cavities. 95% Bonferroni confidence intervals were used to determine selection of forest stand and tree characteristics. Chi-square tests were used to compare cavity characteristics.

Variable	Random		Roost		Bonferroni CI (%)	Selection	
	<i>n</i>	%	<i>n</i>	%			
Forest stand structure							
Tree species							
Red beech	61	50.8	49	81.6	70–93	Select	
Dead beech	15	12.5	7	11.7	2–21	Random	
Silver beech	41	34.2	4	6.7	0–14	Avoid	
Mountain beech	1	0.8	0	0			
Broadleaf	2	1.7	0	0			
Total	120	100	60	100			
Tree characteristics							
Tree species							
Red beech	61	50.8	15	93.8	79–100	Select	
Dead beech	15	12.5	1	6.2	0–20	Random	
Silver beech	41	34.2	0	0			
Mountain beech	1	0.8	0	0			
Broadleaf	2	1.7	0	0			
Total	120	100	16	100			
Cavity characteristics							
Cavity type					χ^2	d.f.	<i>P</i>
Knot	20	51.3	8	40.0			
Split	6*	15.4	5	25.0			
Hollow	11	28.2	4	20.0			
Basal hollow	2*	5.1	3	15.0			
Total	39	100	20	100	1.8	2	0.42
Number of entrances							
1	38	97.4	15	75.0			
>1	1	2.6	5	25.0			
Total	39	100	20	100	40.3	1	<0.001

*Cells combined.

Roost cavities

Mystacina roosts were located at various heights from the ground, and were found in main limbs, trunks, and at the base of trees. The bats did not select a particular type or height of cavity (Tables 1 and 2). Roost cavities had significantly more entrances than random cavities. Twenty-five percent of roosts had more than one entrance, including one that had four entrances (Table 1). Mean cavity volume and internal height were significantly larger in roost cavities than in random cavities, indicating communal *Mystacina* preferred to roost in relatively large cavities. No other cavity characteristics measured differed significantly from random (Table 2).

Modelling structural characteristics of roost trees and roost cavities*Tree characteristics*

Initially, all six tree variables were entered into the stepwise logistic regression analysis of tree characteristics. The best model indicated that three variables explained the variation between *Mystacina* roost trees and random trees. The probability of *Mystacina* roosting in a tree increased as trunk height and number of cavities increased and as canopy cover decreased (Table 3). This model correctly classified roosts and random trees 69 and 99% of the time, respectively, and the Hosmer & Lemeshow lack-of-fit test suggested a relatively good fit of the model to these data ($\chi^2 = 6.5$, d.f. = 8, $P = 0.595$).

Table 2 Characteristics (continuous variables) of forest stand structure, trees, and cavities used by *Mystacina tuberculata* compared with random sites. Analysis of forest stand structure compares trees from 15 plots around roost trees ($n = 60$ trees) with trees from 30 random plots ($n = 120$ trees). Analysis of tree characteristics compares 16 roost trees with 120 random trees, and analysis of cavity characteristics compares 20 roost cavities with 39 random cavities. Sample sizes for individual characteristics vary. Two-sample *t*-tests were used to compare variables, and variables are expressed as means ± 1 SD. DBH, diameter at breast height; DCH, diameter at cavity height.

Variable	Roost			Random			<i>P</i>
	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range	
Forest stand structure							
Stem density per plot (stems/ha)	15	252.9 \pm 135.6	114–647	30	411.8 \pm 273.4	64–1294	0.01
Canopy cover/plot (%)	15	77.3 \pm 12.3	50–95	30	83.9 \pm 10.5	50–95	0.08
Tree characteristics							
Canopy cover (%)	15	76.3 \pm 13.4	60–95	119	83.9 \pm 14.2	40–100	0.05
DBH (cm)	16	104.5 \pm 25.5	67–161	120	54.8 \pm 28.4	20–160	<0.001
Trunk height (m)	15	20.0 \pm 5.5	11–29	120	10.3 \pm 5.3	1–26	<0.001
Tree height (m)	16	33.9 \pm 5.4	20–40	120	22.3 \pm 9.7	2–45	<0.001
Number of cavities*	14	3.7 \pm 2.5	1–9	120	0.7 \pm 1.1	0–5	<0.001
Cavity characteristics							
DCH (cm)	20	88.2 \pm 23.7	60–140	38	75.2 \pm 21.5	23–125	0.04
Height from ground (m)	20	10.0 \pm 5.3	1–23	39	9.2 \pm 5.8	0–21	0.61
Horizontal vegetation clutter (m)	16	5.4 \pm 3.2	1.1–11.5	38	5.4 \pm 2.4	0.5–11.0	0.58
Vertical vegetation clutter (m)	16	5.4 \pm 2.2	1.0–9.0	38	4.9 \pm 2.8	0.5–12.0	0.35
Entrance area (cm ²) [†]	22	558.5 \pm 876.4	45–3000	39	407.0 \pm 721.9	15–36 000	0.27
Inside cross-sectional area (cm ²) [†]	17	898.2 \pm 922.9	120–3750	39	739.1 \pm 1032.8	50–4400	0.16
Internal height (cm)	17	129.0 \pm 72.9	0–280	39	64.9 \pm 102.0	0–500	0.02
Internal depth (cm) [†]	17	66.8 \pm 125.9	0–500	39	41.8 \pm 75.4	0–300	0.96
Volume (m ³) [†]	17	0.3 \pm 0.6	0.02–2.6	39	0.2 \pm 0.6	<0.01–2.5	<0.01
Wall thickness (cm)	17	30.2 \pm 11.3	15–45	39	25.4 \pm 11.8	3–58	0.16

*Compared using Mann-Whitney *U*-test. [†]Transformed for analysis by log *x* or log(*x* + 1).

Table 3 Best fit model for logistic regression of trees used by *Mystacina tuberculata* and random trees.

Variable	Coefficient	SE	Wald's χ^2	d.f.	P	Odds ratio
Constant	-3.947	2.830	1.945	1	0.163	0.019
Canopy closure	-0.064	0.034	3.497	1	0.061	0.938
Number of cavities	1.210	0.377	10.278	1	0.001	3.353
Trunk height	0.329	0.095	12.050	1	0.001	1.389

Table 4 Best fit model for logistic regression of cavities used by *Mystacina tuberculata* and random cavities.

Variable	Coefficient	SE	Wald's χ^2	d.f.	P	Odds ratio
Constant	-1.644	0.536	9.417	1	0.002	0.193
Number of entrances*	3.481	2.131	2.668	1	0.102	32.507
Inside cross-section	-0.002	0.001	6.172	1	0.013	0.998
Internal cavity height	0.002	0.001	7.610	1	0.006	1.002

*Categorical variable, cavities coded as having either 1 or >1 entrance.

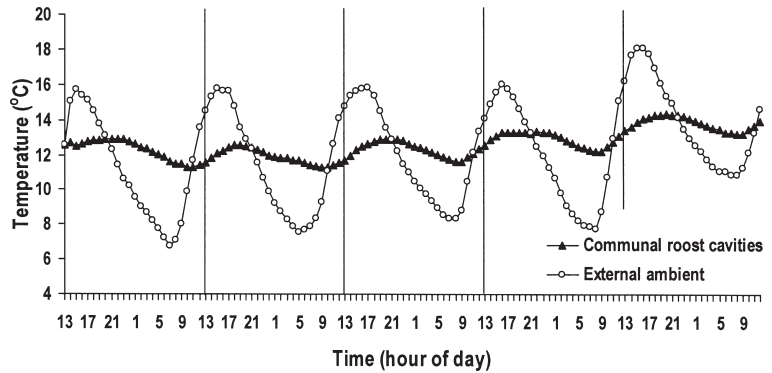
Table 5 Best fit model for logistic regression of trees used as roosts by either *Mystacina tuberculata* or *Chalinolobus tuberculatus*.

Variable	Coefficient	SE	Wald's χ^2	d.f.	P	Odds ratio
Constant	0.014	0.004	12.249	1	0.000	1.014
Distance from edge	-4.600	1.065	18.653	1	0.000	0.010

Table 6 Best fit model for logistic regression of cavities used as roosts by either *Mystacina tuberculata* or *Chalinolobus tuberculatus*. DCH, diameter at cavity height.

Variable	Coefficient	SE	Wald's χ^2	d.f.	P	Odds ratio
Constant	-7.964	3.215	6.135	1	0.013	0.000
Height from ground	-0.279	0.143	3.809	1	0.051	0.757
DCH	0.184	0.091	4.144	1	0.042	1.202
Entrance area	0.012	0.007	3.116	1	0.078	1.012
Internal cavity depth	0.001	0.001	3.657	1	0.056	1.001
Internal cavity height	0.004	0.001	5.779	1	0.016	1.004
Wall thickness	-0.321	0.186	2.987	1	0.084	0.726

Fig. 1 Average hourly temperature recorded in communal *Mystacina tuberculata* roosts ($n = 10$) compared with external ambient temperature over 5-day periods during January–February. Recording began at 1200 h and data points are shown in 1-h increments, where 13 = 1201–1300 h, etc.



Cavity characteristics

Eleven of the 12 cavity variables were entered into the initial logistic regression analysis of cavity characteristics. Cavity volume was not included in the model because it was derived from three other variables. The best model consisted of three variables explaining a significant proportion of the variation between *Mystacina* roost cavities and random cavities. *Mystacina* were more likely to roost in a cavity as number of entrances and interior cavity height increased and as internal cross-sectional area became narrower (Table 4). This model correctly classified *Mystacina* roost cavities and random cavities 46 and 95% of the time, respectively, and the Hosmer & Lemeshow lack-of-fit test suggested the model fitted these data reasonably well ($\chi^2 = 7.6$, d.f. = 8, $P = 0.468$).

Temperature inside *Mystacina* roosts

Temperature was measured inside 10 unoccupied communal roost cavities and compared with ambient temperature. Temperatures inside roost cavities were stable relative to ambient temperature, which fluctuated greatly during the 5-day sampling periods (Fig. 1). The mean temperature range inside roost cavities ($2.3 \pm 1.6^\circ\text{C}$), was significantly less than ambient temperature range ($9.4 \pm 2.4^\circ\text{C}$) ($t = 10.16$, d.f. = 9, $P < 0.001$). Roost cavity maximum temperatures were significantly cooler (by $3.6 \pm 2.3^\circ\text{C}$), and roost minimum temperatures were significantly warmer (by $3.4 \pm 2.2^\circ\text{C}$), than ambient temperatures (paired t -tests, $P < 0.001$). Roost temperatures also changed at a slower rate per hour than ambient temperatures ($t = 9.67$, d.f. = 9, $P < 0.001$). On average, the maximum temperature inside roosts occurred at $1830 (\pm 2.5)$ h, a significant delay of 3.2 ± 2.8 h from the time at which ambient temperature peaked (1530 ± 0.7 h) ($t = 3.5$, d.f. = 9, $P < 0.006$). Maximum temperature in roosts was

then stable for 6.3 ± 3.2 h, significantly longer than ambient maximum temperature (1.9 ± 1.3 h) ($t = -5.4$, d.f. = 9, $P < 0.001$).

Mystacina roosting behaviour

Communal roosts were occupied for a mean of 5.6 ± 6.9 days per visit ($n = 23$, range = 1–32 days) and frequently reused. Three roosts were used twice in one particular season, and at least four roosts were used for more than one season. Two of these four roosts were used over three seasons. The size of colonies varied, averaging 310 ± 88.1 bats (range = 103–468, $n = 40$ video-nights). A total of 529 bats were caught in harp traps over six capture sessions at five different roosts. Only a small proportion of emerging bats were caught at each roost, and it was not possible to estimate the total number of bats emerging. Number of captures at each roost ranged from 25–133 individuals, on average comprising $29.9 \pm 17.9\%$ adult males, $14.2 \pm 13.6\%$ breeding females, $8.3 \pm 6.1\%$ non-breeding females, and $47.6 \pm 26.9\%$ juveniles.

Comparisons with *Chalinolobus*

Seven variables (six tree characteristics, plus distance from forest-grassland edge) were entered into a stepwise logistic regression to examine which characteristics explained most of the structural variation between *Mystacina* and *Chalinolobus* roost trees. The best model indicated that only one variable (distance from forest-grassland edge) accounted for a significant proportion of the variation (Table 5). So although the trees used by the two species were very similar (large old red beech trees), *Mystacina* was more likely to roost in trees farther from the forest-grassland edge. The model classified *Mystacina* roost trees and *Chalinolobus* roost trees 62 and 98% of the time, respectively, and the Hosmer & Lemeshow lack-of-fit test suggested a

relatively good fit of the model to these data ($\chi^2 = 7.4$, d.f. = 8, $P = 0.496$).

Nine variables were entered into the logistic regression analysis of cavity characteristics. The two measures of vegetation clutter outside roost entrance were not included in the model, because they caused an unacceptable reduction in the total number of cases the model could analyse. The best model indicated that six variables explained most of the variation between *Mystacina* and *Chalinolobus* roost cavities. *Mystacina* were more likely to roost in cavities lower to the ground and with thinner walls, and larger DCH, entrance area, internal height and depth (Table 6). This model correctly classified *Mystacina* and *Chalinolobus* roost cavities 63 and 98% of the time, respectively, and the Hosmer & Lemeshow lack-of-fit test suggested a good fit of the model to these data ($\chi^2 = 5.0$, d.f. = 7, $P = 0.666$).

DISCUSSION

Evidence for roost site selection

Communally occupied *Mystacina* roost sites in the Eglinton Valley were distinctive from random available sites. *Mystacina* roosted in more open parts of the forest. Like *Chalinolobus*, they selected roosts in some of the largest red beech trees available. Several species of bats inhabiting temperate forests select roosts in sites with similar characteristics to those selected by *Mystacina*. *Chalinolobus*, and three species of bat found in North America, preferred to roost in open stands that had lower stem densities and canopy closure than other parts of the forest (Betts 1995; Vonhof & Barclay 1996; Brigham et al. 1997; Sedgeley & O'Donnell 1999a). While tree spacing around the roost site may be important in itself, it may be that openness of habitat is correlated with increased tree size (Vonhof & Barclay 1996; Brigham et al. 1997). Therefore, it has been suggested that bats may be selecting for one or both of these features (Brigham et al. 1997). Openness of roosting habitat would increase manoeuvrability around, and access to and from, roosts (see below). It has also been suggested that roost trees in open areas may contribute to increased solar exposure of roost cavities, creating warmer temperatures that may benefit reproductive females (Brigham et al. 1997). This seems unlikely in this study because roost cavities of *Mystacina* and *Chalinolobus* were situated below the canopy.

Many bat species, including *Mystacina* and *Chalinolobus*, select roost trees that are larger than the average available trees (Vonhof & Barclay 1996; Menzel et al. 1998; Rabe et al. 1998; 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 has been shown to increase with stem diameter (Bennett et al. 1994), and large old trees with bigger surface areas are likely to be more susceptible to weathering and cavity formation. Roost trees of *Mystacina* and *Chalinolobus* were both larger, and contained more cavities, than random trees (Sedgely & O'Donnell 1999a; this study). It is also possible that larger trees provide greater insulation to roosting bats, thereby reducing their thermoregulatory costs (see below).

Did *Mystacina* and *Chalinolobus* partition their roosting habitat?

Structural characteristics of roosting habitat

In the Eglinton Valley, *Mystacina* used roost trees with features similar to *Chalinolobus*, but roosts were all inside the forest and were farther from the forest-grassland edge than those of *Chalinolobus*. A possible explanation for this difference is that the bats chose to roost close to their respective foraging areas. In the Eglinton Valley, *Mystacina* spends a large proportion of its time foraging within forest, whereas *Chalinolobus* forages more along forest edges and open shrubland habitats (O'Donnell et al. 1999; O'Donnell 2000a; J. Christie unpubl. data). However, *Mystacina* has also been recorded commuting to foraging areas over open grassland (O'Donnell et al. 1999).

Mystacina was probably more tolerant of vegetation clutter around roosts than *Chalinolobus*. The height of *Mystacina* roosts from the ground and distance to nearest vegetation clutter outside roost entrances did not differ from random cavities. In comparison, *Chalinolobus* selected roost cavities where distance to nearest vegetation clutter was greater than random cavities, and roosts that were significantly higher from the ground than both random cavities and *Mystacina* roost cavities (cf. Sedgely & O'Donnell 1999b). Differences in echolocation call structure and morphology between the two bat species may explain why *Mystacina* is more likely to be tolerant of vegetation clutter. *Mystacina* has wide-bandwidth multiharmonic echolocation calls with peak amplitude of 27–28 kHz. Compared with *Chalinolobus*, these calls were

more typical of bat species that glean insect prey and were more suited to flying within cluttered forest habitats. The agility of *Mystacina* on the ground and trunk surfaces would add to its manoeuvrability in cluttered habitat (Daniel 1990). *Chalinolobus* has longer duration echolocation calls with peak amplitude of 36–40 kHz (Parsons 1997; Parsons et al. 1997) and a wing shape with average wing loading and aspect ratio typical of aerial insectivores with moderate to fast flight speeds and limited manoeuvrability within dense vegetation (O'Donnell 2000a).

Mystacina differed from *Chalinolobus* in their selection of cavity type. *Mystacina* roosted in relatively large trunk hollows. Sizes of entrances and some internal dimensions were significantly larger than those of random cavities and the knot-hole cavities used by *Chalinolobus*. *Mystacina* may simply choose to roost in large cavities that accommodate their significantly larger group sizes. In this study, the largest *Mystacina* group was 468 bats, but the largest *Chalinolobus* group was 123 bats (mean = 35 bats; O'Donnell & Sedgeley 1999). The maximum roosting group size recorded for *Mystacina* is 6977 bats (Lloyd 2001). Factors affecting differences in communal roost group size between the two species may include differences in social and reproductive behaviour (Daniel 1990; O'Donnell 2000b, 2002). Roost cavities used by *Mystacina* also had a greater number of entrances than random cavities and *Chalinolobus* roosts. *Mystacina* may choose this characteristic to better facilitate movements of large numbers of individuals in and out of roosts, especially since activity at roosts continues for >80% of the night (O'Donnell et al. 1999; Sedgeley 2001b). Alternatively, multiple entrances may be an incidental function of large cavity formation.

Roost temperature and thermal qualities

Roosts of both species had similar thermal properties, with roosting cavities being insulated from ambient conditions. Several studies have noted reduced temperature ranges, and lags in temperature change inside tree roosts compared with ambient conditions or non-roosts (Maeda 1974; Calder et al. 1983; Alder 1994; Vonhof & Barclay 1997; Sedgeley 2001a). These phenomena have been attributed to the structural properties of the roost (reviewed in Sedgeley 2001a). Most of these studies, for example, noted a correlation between increasing stem diameter and increased insulation or temperature lag. The insulative properties of

wood increase with stem diameter and bark thickness (Nicolai 1986), and large diameter red beech trees (selected by *Mystacina* and *Chalinolobus*) have thicker bark than other beech trees (Wardle 1984). Therefore, both bat species may be selecting roost sites with structural characteristics that are best able to provide a stable thermal environment.

Chalinolobus roost temperature data were gathered from maternity roosts (i.e., roosts in which females congregate to give birth and rear young, Sedgeley 2001a). *Mystacina* roosts in this study were also dominated by breeding females and young. Selection of maternity roosts with warm stable temperatures allows breeding females to reduce their energy expenditure while remaining active and homeothermic for longer periods. This in turn results in an increased rate of gestation, post-natal growth and, ultimately, over-winter survival (Racey 1982; Kunz 1987; Zahn 1999). Temperatures in the roosts of both bat species reached maxima late in the day and remained warm throughout the night, thus benefiting non-volant young that were left alone in the roost while females foraged. It was not possible to measure temperature inside roosts while they were occupied, but it is likely that the larger numbers of *Mystacina* able to cluster in the large cavities would markedly increase the temperature inside by generating higher levels of metabolic heat (Kurta 1985, 1986). Additionally, more heat could be generated because individual *Mystacina* have larger body masses than *Chalinolobus* (O'Donnell et al. 1999; O'Donnell 2001).

Mystacina and *Chalinolobus* from the Eglinton Valley appear to have different thermoregulation and energy conservation strategies, which might influence choice of roost site and roosting behaviour. Webb (1999) suggested that there are differences in use of daily torpor between the two species. Open flow respirometry techniques showed that captive *Mystacina* were better insulated and expended relatively less energy to remain non-torpid at low temperatures than did *Chalinolobus*, and that *Chalinolobus* entered deeper torpor than did *Mystacina*. Temperature sensitive transmitters showed that free-living *Mystacina* remained active and never entered torpor when roosting communally, whereas *Chalinolobus* entered torpor on 35% of days when roosting communally. Both species used torpor to conserve energy when solitary in roosts. Sample sizes in this study were relatively small and included only non-reproductive bats, but Webb (1999) cautiously suggested that: (1) because

Chalinolobus saves much more energy by using torpor than *Mystacina* (especially at low temperatures) it is likely they will use torpor more frequently than *Mystacina* in the wild; and (2) because roosting group size is much smaller in *Chalinolobus* than in *Mystacina* it is easier for *Chalinolobus* to enter torpor within a communal roost. The thermoregulation and energy conservation strategies used by the two species and the thermal properties of their roosts require further investigation.

Roosting behaviour

Tree-roosting bats move between roost sites more frequently than species occupying other structures. The majority of tree-dwelling bats have short residency times (<5 days), and 50% move every 1–2 days (reviewed in Kunz & Lumsden in press), which may be typical for tree-cavity roosting bats in temperate climatic zones. *Chalinolobus* in the Eglinton Valley spent on average 1.4 days in each communal roost (O'Donnell & Sedgely 1999). *Chalinolobus* used hundreds of different trees over a period of 3 years, which were rarely reused. However, after 8 years, the proportion of original roosts reused rose to 52% in one roosting area (O'Donnell & Sedgely 1999; C. O'Donnell unpubl. data). In comparison, *Mystacina* occupied roosts for relatively long periods of time, which may be more typical of species that use large hollow trunks and often gather in larger groups (O'Donnell & Sedgely 1999). *Mystacina* appeared to have a small number of roosts that the population cycled among, and returned to each year. It is unlikely that the full pattern of roost use was revealed in this study because the sampling period varied each year, but patterns observed in the Eglinton Valley may be typical for *Mystacina*. *Mystacina* in the Rangataua forest also had relatively high levels of roost reuse and site fidelity (Lloyd 2001).

Roosts selection and implications for conservation

Both *Mystacina* and *Chalinolobus* chose to roost in well insulated cavities in the largest and oldest trees available to them. This is perhaps unsurprising since communal roost choice in both species is likely to be constrained by the basic requirements of breeding and rearing young in a temperate climate. The protection of the largest and oldest trees in the forest appears to be crucial for the survival of both bat species. Bats inhabiting temperate zones spend over half of their lives roosting, breeding, and hibernating

within their roost environment (Kunz 1982). Most bat species are secondary cavity users and are not known to excavate their roosts (Kunz 1982), although *Mystacina* may modify roost cavities to some degree (Lloyd 2001). These behaviours make bats particularly vulnerable to reduction in abundance and quality of roosting habitat. Forests that are managed for timber production do not have as many cavity-bearing trees as unmodified forests (Mackowski 1984; Newton 1994; Lindenmayer & Possingham 1995). Therefore, it can be assumed that logging will reduce both abundance of cavities, and range of cavity sizes and quality. Bats can use cavities of a lower quality, but if they do, reproductive success can be reduced (e.g., *Chalinolobus*, O'Donnell 2002). If maternity groups are forced into long-term use of lower quality roosts as a consequence of habitat modification then negative effects on growth, productivity, and survival will accrue, and eventually affect population viability adversely (Brigham & Fenton 1986; Richter et al. 1993; Zahn 1999).

Differences in roost cavity structure and roosting behaviour between *Mystacina* and *Chalinolobus* may influence their relative vulnerability to threats such as habitat loss and predation. *Mystacina* uses cavities with large entrances that are relatively low to ground and a large proportion of the breeding population appears to roost in one tree for a relatively long time period. These behaviours may make it particularly vulnerable to predator attack and to catastrophic events such as tree-fall. Additionally, use of communal roost sites by *Mystacina* seems to include a traditional component. Individual roosts can be used intermittently for several decades (Lloyd 2001). For example, a roost found on Whenua Hou/Codfish Island in 1932 was still being used in 1998 (Stead 1936; J. Sedgely unpubl. data). *Mystacina* in the Eglinton Valley used few trees as communal roosts (<20 trees). If such trees have limited availability then it might be difficult for *Mystacina* to seek out new sites if traditional roosts are lost. *Chalinolobus* by comparison, roosts high in trees, moves to a new roost site almost every day and the population is spread over many roosts on any one day. These behaviours may reduce the effect of terrestrial predators and catastrophic events, but may expose them to other threats. *Chalinolobus* tend to form behaviourally isolated roosting groups within small exclusive roosting areas. If a group's roosting area was largely destroyed it may have limited opportunity to integrate with the residents of a new area if it is already occupied.

CONCLUSIONS

The reasons why *Mystacina* and *Chalinolobus* use different sized roost cavities may be linked to behavioural or energetic requirements, or an interaction of these or other factors. Basic ecomorphological differences between the two species may allow them to use a different range of cavities. Whatever the explanation, the two species do have clear differences in roosting behaviour and roost use. These differences must be considered when undertaking conservation management actions such as the protection and restoration of habitat. To maintain population viability it may be essential to ensure that a sufficient number of trees with a range of cavity types are maintained through logging cycles, and incorporated into reserve design proposals.

This study focused on communal roost use during the summer months in a particular lowland *Nothofagus* forest. To fully understand roosting requirements for both species of New Zealand bat it is necessary to examine roost selection in other habitats and between seasons. For example, areas of podocarp forest are still logged on private land (Ministry of Forestry 1997), and some *Chalinolobus* populations persist in highly developed fragmented landscapes (O'Donnell 2001). To adequately conserve bat populations in these habitat types we need more data describing their roosting ecology. In areas outside the Eglinton Valley, *Mystacina* are very active in winter, and move between numerous roost sites (Sedgeley 2001b). The structural characteristics of roosts used in summer and in winter may differ. Preliminary data suggest that *Mystacina* also uses small-sized cavities for solitary roosts and for mating (singing trees) (O'Donnell et al. 1999; this study). It is likely that a local *Mystacina* population requires a range of cavity sizes, not just the large well insulated cavities used by breeding colonies. Future studies could examine inter- and intraspecific roost use in bats (including roosts used by solitary and non-reproductive bats), and investigate differences among habitat types and seasons.

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