

The abundance, distribution and structural characteristics of tree-holes in *Nothofagus* forest, New Zealand

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Abstract Tree-holes provide an important microhabitat that is used for feeding, roosting and breeding by numerous species around the world. Yet despite their ecological importance for many of New Zealand's endangered species, few studies have investigated the abundance or distribution of tree-holes in native forests. We used complementary ground and climbed tree surveys to determine the abundance, distribution and characteristics of tree-holes in undisturbed *Nothofagus* forest in the Lewis Pass, New Zealand. We found that hole-bearing trees were surprisingly abundant compared with many other studies, including Australian *Eucalyptus* species and American beech. In fact, we estimated as many as 3906 tree-holes per hectare, of which 963 holes per hectare were potentially large enough to provide roost sites for hole-nesting bats in New Zealand, while only eight holes per hectare were potentially suitable for specialist hole-nesting birds. This was of great interest as primary cavity-excavating animals are absent from New Zealand forests, compared with North America and Australia. Moreover, tree-hole formation in New Zealand is likely to be dominated by abiotic processes, such as branch breakage from windstorms and snow damage. As has been found in many other studies, tree-holes were not uniformly distributed throughout the forest. Tree-holes were significantly more abundant on the least abundant tree species, *Nothofagus fusca*, than on either *N. menziesii* or *N. solandri*. In addition to tree species, tree size was also an important factor influencing the structural characteristics of tree-holes and their abundance in this forest. Moreover, these trends were not fully evident without climbed tree surveys. Our results revealed that ground-based surveys consistently underestimated the number of tree-holes present on *Nothofagus* trees, and illustrate the importance of using climbed inspections where possible in tree-hole surveys. We compare our results with other studies overseas and discuss how these are linked to the biotic and abiotic processes involved in tree-hole formation. We consider the potential implications of our findings for New Zealand's hole-dwelling fauna and how stand dynamics and past and future forest management practices will influence the structural characteristics of tree-holes and their abundance in remnant forest throughout New Zealand.

Key words: forest canopy, microhabitat, *Nothofagus*, phytotelmata, tree-hole.

INTRODUCTION

Tree-holes provide important ecological resources for a diverse range of animal species throughout the world (Greeney 2001; Gibbons & Lindenmayer 2002). Tree-holes may be dry or water-filled, with the latter providing both ephemeral and permanent freshwater habitats in the forest canopy that are used by a plethora of aquatic insect species (Kitching 1971; Greeney 2001). Dry tree-holes have been found to be an important resource for a wide range of wildlife species, including numerous species of birds (Elliott *et al.* 1996; Carlson *et al.* 1998; Bai *et al.* 2003), bats

(Sedgeley & O'Donnell 1999a; Kerth *et al.* 2001), marsupials (Lindenmayer *et al.* 1990; Gibbons *et al.* 2002; Russell *et al.* 2003) and snakes (Webb & Shine 1997) that use tree-holes as nesting or roosting sites. In Australia, for example, tree-holes are known to provide nest, den and shelter sites for more than 300 vertebrate species, of which at least 100 are thought to be rare or threatened (Gibbons & Lindenmayer 2002). In New Zealand, comparatively little is known about the fauna of tree-holes. The limited research conducted to date suggests that tree-holes are important nesting and roosting sites for approximately 12 native bird species, two native bats and many exotic bird and marsupial species (Robertson 1985; Sedgeley 2003). Furthermore, many of the native bird and bat species utilizing tree-holes are either endangered or declining in

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numbers (e.g. mohua *Mohoua ochrocephala*, yellow-crowned kakariki *Cyanoramphus auriceps*, long-tailed bat *Chalinolobus tuberculatus* and lesser short-tailed bat *Mystacina tuberculata*) (O'Donnell 1996, 2000; Hitchmough 2002). A major limiting factor in the conservation and management of tree-hole-dwelling fauna in New Zealand is the lack of quantitative knowledge on the abundance, distribution and structural characteristics of tree-holes in remnant forests. So far only a few published studies have investigated the distribution and structural characteristics of tree-holes in New Zealand. Of these studies, most have emphasized habitat usage by vertebrate species (e.g. Sedgely & O'Donnell 1999b), or involved qualitative inspections of insect communities inhabiting selected holes in just one or a few trees (e.g. Taylor & Ewers 2003; Derraik & Heath 2005).

A wide range of factors can influence the development of tree-holes, including individual tree characteristics such as diameter, age, health and growth habit, as well as site features such as stand basal area, slope, topographic position and rainfall (Bennett *et al.* 1994; Lindenmayer *et al.* 2000; Whitford 2002; Fan *et al.* 2003). The intrinsic traits of particular tree species also play an important role in influencing the distribution and abundance of tree-holes. For example, wood density is the single most important factor determining mechanical breaking strength (Persson *et al.* 1995; Beets *et al.* 2001). Wood density can be highly variable across different tree species and undoubtedly influences branch shedding, subsequent fungal attack and rot. Similarly, different tree species have unique growth responses to damage, with species-specific 'grow-over' reactions to limb breakage and scarring leaving some species more susceptible to rot than others (e.g. *Nothofagus*, Wardle 1984; Sessile oak, *Quercus versicolor*, Guilley *et al.* 2004). Size and age structure of the forest, logging practices and habitat fragmentation can also influence the distribution and abundance of tree-holes.

In addition, tree-hole abundance and distribution are influenced by many abiotic and biotic factors which differ among biogeographic regions. For example, in many Northern Hemisphere forests tree-holes are largely formed by primary cavity-excavating species, such as woodpeckers. Conversely, woodpeckers do not occur in Australia; however, there are several species of parrot and cockatoo, as well as many marsupials and invertebrates that excavate both decayed and sound wood (Gibbons & Lindenmayer 2002). However, as none of these animals initiate cavity excavation, large tree-holes suitable for vertebrate fauna can take more than 200 years to form (Gibbons & Lindenmayer 2002). Fire is also an important factor in tree-hole formation in Australia (Gibbons & Lindenmayer 2002). Tree-holes form when heartwood decay is present and a tree is exposed to some sort of physiological or physical stress, such as fire, increasing tree age

and subsequent branch shedding, or damage from insects (Gibbons & Lindenmayer 2002). Tree-hole formation processes in New Zealand forest ecosystems are likely to differ dramatically from those in the Northern Hemisphere and, to a lesser extent, Australia. Primary cavity-excavating vertebrates are absent from New Zealand and instead abiotic factors play the essential role in cavity development. However, unlike in Australia where fire is an important abiotic factor stimulating tree-hole formation in *Eucalyptus* forests, windstorms and snow damage are likely to be more important in New Zealand. In New Zealand forest ecosystems, wounding (such as mechanical-scarring or incomplete branch abscission) from storm events or heavy snowfall predisposes trees to the slow decay processes instigated by fungal and invertebrate attack, eventually leading to the formation of tree-holes (Stewart & Burrows 1994). Despite these differences, most of our current knowledge on tree-holes in Southern temperate regions comes from studies in Australia's *Eucalyptus* forests.

Given the substantial difference in the relative importance of processes involved in tree-hole formation in different biogeographic regions, it is therefore difficult to determine *a priori* whether individual tree characteristics (e.g. tree size, age and tree species) will have the same influence on the abundance and distribution of tree-holes in New Zealand forest ecosystems, as elsewhere in the world. Thus, the purpose of this paper is to present the first comprehensive and systematic investigation of the abundance, distribution and structural characteristics of tree-holes within temperate southern beech (*Nothofagus*) forest in New Zealand. Specifically, we investigated: (i) variation in the abundance, distribution and structural characteristics of tree-holes among tree species; (ii) variation in the abundance and structural characteristics of tree-holes in relation to individual tree traits; and (iii) the degree of difference between ground-based and climbed survey techniques that may allow an estimate of potential bias in future rapid-assessment surveys of tree-hole abundance.

METHODS

Study site

This study was undertaken in a southern temperate mixed-beech forest within the Lewis Pass National Reserve, South Island, New Zealand, in April and September 2004. The Lewis Pass National Reserve is part of the largest continuous forest remaining in New Zealand today, at over one million hectares in extent. The study area was situated at the convergence of the Nina and Lewis Rivers, at ca 700 m a.s.l. (42°28'S, 172°23'E). This area of New Zealand has an average rainfall of 1900–2000 mm per annum (Stewart *et al.*

1991), with winter minimum and summer maximum air temperatures of -7°C and 32°C , respectively (Stewart *et al.* 1991; Stewart & Burrows 1994).

The Nina Valley is glacial in origin, with mountain beech (*Nothofagus solandri* var. *cliffortioides*) dominating the flora at the timberline (ca 1300 m a.s.l.), giving way to silver beech (*N. menziesii*) at lower elevations and mixtures of silver and red beech (*N. fusca*) on the lower slopes and river flats (Hosking & Kershaw 1985). The forest understorey is open, with extensive moss and leaf litter cover on the ground. *Nothofagus* seedlings dominate the understorey, with broadleaf (*Griselinia littoralis*), lancewood (*Pseudopanax crassifolius*), *Myrsine divaricata* and *Coprosma* spp. also present (Hosking & Kershaw 1985).

Ground-based tree-hole survey

A 0.36-ha portion of the study area was subdivided into 36 contiguous, 10×10 m subplots, for systematic sampling. The 3600-m² plot was established by randomly selecting a starting point, the south-western corner, and then measuring 60 m in both a northerly and an easterly direction to create a square. Within each subplot, tree species (dead *Nothofagus* spp., or live *N. fusca*, *N. menziesii* or *N. solandri*) and trunk diameter at breast height (d.b.h. at 1.4 m) were recorded for all trees ≥ 10 cm d.b.h., in April 2004. Dead *Nothofagus* trees were only included in the ground survey if they had an erect trunk greater than 1.4 m in height. Where trees had multiple stems at breast height, the d.b.h. was taken below the initial stem split.

Tree-holes with an entrance height, width or horizontal depth into the trunk of less than 1 cm were excluded from both the ground and climbed surveys, due to time constraints and the large number of potential holes likely to fall into this size category. Furthermore, tree-holes were only recorded if they penetrated at least into the outer sapwood, rather than simply representing a deformation in the tree bark. Two teams of three randomly selected surveyors circumnavigated each tree, scanning it with binoculars and recording the total number of holes visible from the ground, as well as the height (m), location (branch, trunk or fork) and aspect (0, 90, 180 or 270°) of each individual tree-hole. Once a possible tree-hole was detected, it was only formally recorded if all three surveyors agreed that it met the pre-defined criteria described above. Furthermore, each team surveyed all trees in 18 randomly selected 10×10 subplots, covering the full range of tree sizes and species present. For these reasons, the potential for individual observer bias is minor and consistent across the three tree species and all size categories. Hole heights were measured with a handheld clinometer and tape measure.

Climbed tree inspections

Trained arborists surveyed ten live trees of each of the three *Nothofagus* species (*N. fusca*, *N. menziesii* and *N. solandri*) using single-rope climbing techniques (Barker & Standridge 2002), in April and September 2004. Dead *Nothofagus* trees were not climbed, to ensure safe climbing practices. Climbable trees (i.e. ≥ 20 cm d.b.h. and with multiple large branches in the upper canopy) were selected using a random walk through the study area. The random walk began at the south-eastern corner of the 3600-m² study area. Each tree was selected by generating a random compass bearing and walking a random number of metres (1–60, using the seconds hand on a watch), following which the nearest climbable tree, of any of the three *Nothofagus* species, was selected until ten of each species had been climbed. If the random walk took the arborists outside the study plot, or no climbable trees were available at the selected point, a new random bearing and distance were generated. A climbing rope was placed at the highest possible point within each tree and arborists systematically surveyed the trunk and all branches for tree-holes. All information about the tree-holes was communicated to a recorder on the ground, yet kept confidential from the other surveyors until the ground surveys had been completed (refer to Harper *et al.* 2004).

The total number of holes, the height of each and their location and aspect were recorded to compare with ground surveys. Additionally, the internal (vertical and horizontal depths, cm) and external (height and width, cm) dimensions were recorded for each tree-hole. From these measurements, the minimum entrance and internal dimensions were derived using the smallest of the height or width and horizontal or vertical depths, respectively. Internal and external measures made in the field were also used to calculate hole entrance area (cm²) and internal volume (cm³) using standard formulas that treated tree-holes as ellipses. Entrance angle (° from vertical) was also recorded for each tree-hole, with vertical holes being recorded as 0°, holes overhanging and facing towards the ground recorded as negative angles, and those facing upwards recorded as positive angles.

The internal conditions considered important for tree-hole inhabiting fauna were recorded (i.e. the presence of standing water, *vs.* damp or dry) in April and September 2004 (early austral Autumn and Spring, respectively). Rainfall is fairly constant throughout the year in the Lewis Pass, with monthly averages of 161 and 177 mm in April and September, respectively (long-term data, 1971–2000, National Institute of Water and Atmospheric Research 2007). Therefore, even though the internal conditions in tree-holes were measured at two discrete time periods, we expect that this was representative of the presence of standing

water in the Lewis Pass, except perhaps for the hottest periods in mid-summer. Lip size (cm) at the lower edge of each tree-hole was also recorded, as this was considered to be a possible determinant of microclimatic conditions inside the hole (e.g. ability to retain standing water).

Statistical analyses

Ground-based survey

An analysis of covariance (ANCOVA) was used to test the main and interactive effects of the four *Nothofagus* tree species categories (dead, *N. fusca*, *N. menziesii*, *N. solandri*) and tree size (d.b.h., covariate) on the number of tree-holes observed on the 423 ground-surveyed trees in the 36 10 × 10 m subplots.

Ground-based survey versus climbed tree inspections

To compare the accuracy of ground-based surveys and climbed inspections, ANCOVA was used to compare the numbers of tree-holes identified from ground-based surveys *versus* climbed inspections on trees of varying size (d.b.h., covariate). Only trees that were both climbed and surveyed from the ground ($n = 30$) were used in analyses. Chi-squared contingency tables were used to determine whether ground-based surveys over- or under-estimated the number of tree-holes among different aspects (0°, 90°, 180°, 270°), locations (trunk, branch, fork) or arbitrarily assigned height categories (0–4.9, 5–9.9, 10–14.9 or 15–19.9 m above ground), relative to the climbed inspections.

Tree-hole characteristics

We used ANCOVA to explore the main and interactive effects of tree species and size (d.b.h., covariate) on the number of tree-holes identified during the climbed inspections. Type-I mixed-effects general linear models (GLMs) were used to explore separately the amount of variation in tree-hole volume and entrance area explained by the fixed effect of tree species (*N. fusca*, *N. menziesii* and *N. solandri*), the random effect of variation in hole size among individual trees within each tree species (tree identity) and the fixed covariate effect of tree size (d.b.h.). Tree-hole volume and entrance area were ln-transformed prior to analyses to meet assumptions of normality and homogeneity of variances (Quinn & Keough 2002). The covariate d.b.h. was ln-transformed prior to analyses. Mixed-effects models were used with Type-I sums of squares because of the hierarchical design of the survey in

which there was dependence among individual holes within trees. Thus, individual hole volumes and entrance areas within trees were not treated as independent replicates. In mixed-effects GLMs, the error degrees of freedom in *F*-ratio tests involving random treatment effects are calculated using the Satterthwaite (1946) method of denominator synthesis which can yield non-integer values.

Pearson's correlations were used to test whether tree d.b.h., tree-hole height, entrance size (entrance area and minimum entrance dimensions) or internal measurements (volume and minimum internal dimensions) were linearly related to each other. Chi-squared contingency tables were used to determine whether holes were equally distributed among branches and trunks, or if they were more likely to occur on N, E, S, W aspects, for the 30 climbed *Nothofagus* trees. Chi-squared contingency tables were also used to test if tree species, d.b.h., hole aspect, location or lip size influenced the internal conditions of tree-holes (i.e. wet *vs.* dry). Forks were excluded from the analyses and tree-holes containing standing water were combined with damp holes to meet the recommended statistical assumption that no more than 20% of the categories had expected frequencies of less than five.

All analyses were performed in Statistica version 7 (StatSoft 2003). Response and predictor variables were $\ln(x + 1)$ transformed where necessary to meet assumptions of normality and homogeneity of variances (Quinn & Keough 2002).

RESULTS

Ground-based surveys

A total of 423 *Nothofagus* trees (≥ 10 cm d.b.h.) were recorded in the ground-based survey of the 36 subplots. Of these, *N. solandri* was the most abundant species comprising 48% of the total trees surveyed, followed by *N. menziesii* (29%), dead *Nothofagus* spp. (16%) and *N. fusca* (7%). Trees were highly variable in size, ranging from 10.0 to 87.8 cm d.b.h.; however *N. fusca* trees were significantly larger (34.8 ± 6.4 cm d.b.h.) than dead *Nothofagus* spp. or live *N. menziesii* and *N. solandri* trees in the study area (22.9 ± 2.8 , 20.3 ± 1.8 and 22.9 ± 1.6 cm d.b.h., respectively) (one-way ANOVA, ln-transformed d.b.h., species effect: $F_{3, 420} = 13.84$, $P < 0.001$). Although *N. solandri* was the most common canopy species, large specimens were rare in the study area (1% of *N. solandri* were ≥ 50 cm d.b.h.). Large dead *Nothofagus* and *N. menziesii* were also relatively rare in the study area (3% of dead *Nothofagus* and 4% of *N. menziesii* were ≥ 50 cm d.b.h.), while *N. fusca* was more evenly distributed across the five size-classes and was the dominant mid-

Table 1. Distribution of tree-holes identified on 423 *Nothofagus* trees (≥ 10 cm d.b.h.) during a ground-based survey of 36 10×10 m contiguous subplots in the Lewis Pass National Reserve, April 2004

Species	No. of trees	Proportion of trees in d.b.h. (cm) class					Prop. with holes	Mean (SE) no. holes/tree
		10–19.9	20–29.9	30–39.9	40–49.9	≥ 50		
Dead trees	67	0.54	0.22	0.15	0.06	0.03	0.45	1.2 (0.3)
<i>N. fusca</i>	30	0.20	0.30	0.20	0.10	0.20	0.74	2.6 (0.5)
<i>N. menziesii</i>	125	0.62	0.24	0.05	0.05	0.04	0.42	0.8 (0.1)
<i>N. solandri</i>	201	0.41	0.41	0.15	0.02	0.01	0.29	0.4 (0.1)
Total	423	0.48	0.33	0.12	0.04	0.03	0.39	0.7 (0.1)

‘Prop. with holes’ indicates the proportion of trees containing holes.

to large-sized canopy tree at this site (50% of *N. fusca* were ≥ 30 cm d.b.h.; Table 1).

A total of 340 tree-holes were observed from the ground on the 423 *Nothofagus* trees surveyed within the study plot. Although *N. fusca* was the least abundant tree species in the study area, most (74%) of the trees were hole-bearing (Table 1). Furthermore, *N. fusca* had many more tree-holes per tree (2.6 ± 0.5 , $n = 31$) than the other *Nothofagus* species (Table 1). By contrast, *N. solandri* was the most common canopy species yet it had the fewest holes per tree (0.4 ± 0.1 , $n = 205$) with proportionally fewer trees containing visible holes (29%; Table 1). However, the main effect of tree species (ANCOVA, ln-transformed tree-hole count, tree species main effect: $F_{3,415} = 0.92$, $P = 0.430$) was not directly interpretable because of significant variation in the covariate of tree size (d.b.h.) between different tree species (ANCOVA, ln-transformed tree-hole count, d.b.h. main effect: $F_{1,415} = 53.55$, $P < 0.001$; tree species \times d.b.h. interaction effect: $F_{3,415} = 3.74$, $P = 0.010$). Significantly more tree-holes were identified from the ground in large *N. fusca* trees than in small *N. fusca* trees, whereas similar numbers of tree-holes were observed in *N. solandri* regardless of d.b.h.

Ground-based survey versus climbed tree inspections

In contrast to the 340 tree-holes identified during the ground-based surveys of 423 trees, the direct, climbed inspections revealed 304 tree-holes on just 30 of these same *Nothofagus* trees. Thus, significantly more tree-holes were found through the climbed inspections (10.1 ± 1.4 /tree) than were identified on the same trees during the ground-based surveys (2.8 ± 0.5 /tree; paired t -test: $t_{\text{calc}} = 7.45$, $n = 30$, $P < 0.001$). Importantly though, there was a significant positive correlation in the number of holes per tree between the two techniques ($r = 0.50$, $n = 30$, $P = 0.005$). ANCOVA confirmed that d.b.h. did not influence the degree of underestimation of tree-hole counts in ground-based surveys (ANCOVA, ln-transformed tree-hole count,

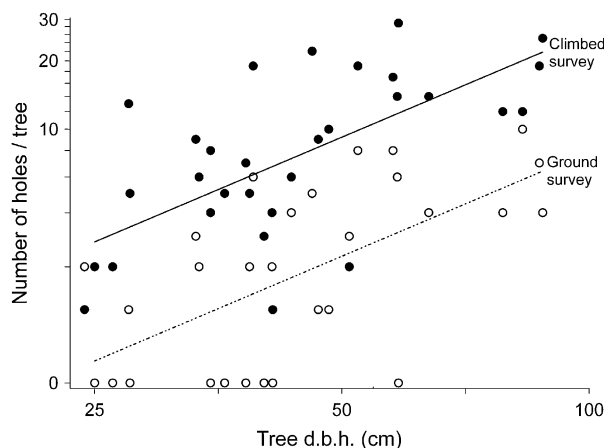


Fig. 1. Comparison of the number of tree-holes identified from the ground-based survey (open circles and dotted fitted line) and climbed direct-inspections (closed circles and solid fitted line) of 30 *Nothofagus* trees of differing sizes (d.b.h.) in the Lewis Pass National Reserve, in April and September 2004. Note that the y-axis is plotted on a logarithmic scale. The equations of the fitted lines are: $\ln(y) = -4.388 + 1.428 \cdot \ln(x)$ (for ground-based counts) and $\ln(y) = -3.263 + 1.428 \cdot \ln(x)$ (for climbed-inspection counts).

survey type \times d.b.h. interaction: $F_{1,56} = 0.01$, $P = 0.990$; Fig. 1).

In addition to underestimates of tree-hole numbers, the ground-based survey also inadequately identified where the holes were found on the *Nothofagus* trees. The number of tree-holes on branches were significantly underestimated from the ground-based survey (18%), compared with climbed inspections (36%) ($\chi^2_{(2)} = 10.17$, $P < 0.001$). Furthermore, tree-holes located in the 10.0–14.9 m hole height category were harder to detect using the ground-based surveys than the climbed inspections, thus the number of holes higher up the trees was significantly underestimated from the ground ($\chi^2_{(3)} = 27.57$, $P < 0.001$).

Tree-hole characteristics

Internal dimensions were measured for 290 of the 304 tree-holes identified during the climbed inspections.

The volume of tree-holes varied markedly among these 290 holes, from the smallest measurable hole of only 0.5 cm³ up to the largest, six orders of magnitude greater, at more than 477 000 cm³. However, large holes were relatively rare and all *Nothofagus* trees contained predominantly small tree-holes (0–999 cm³ volumes; Fig. 2).

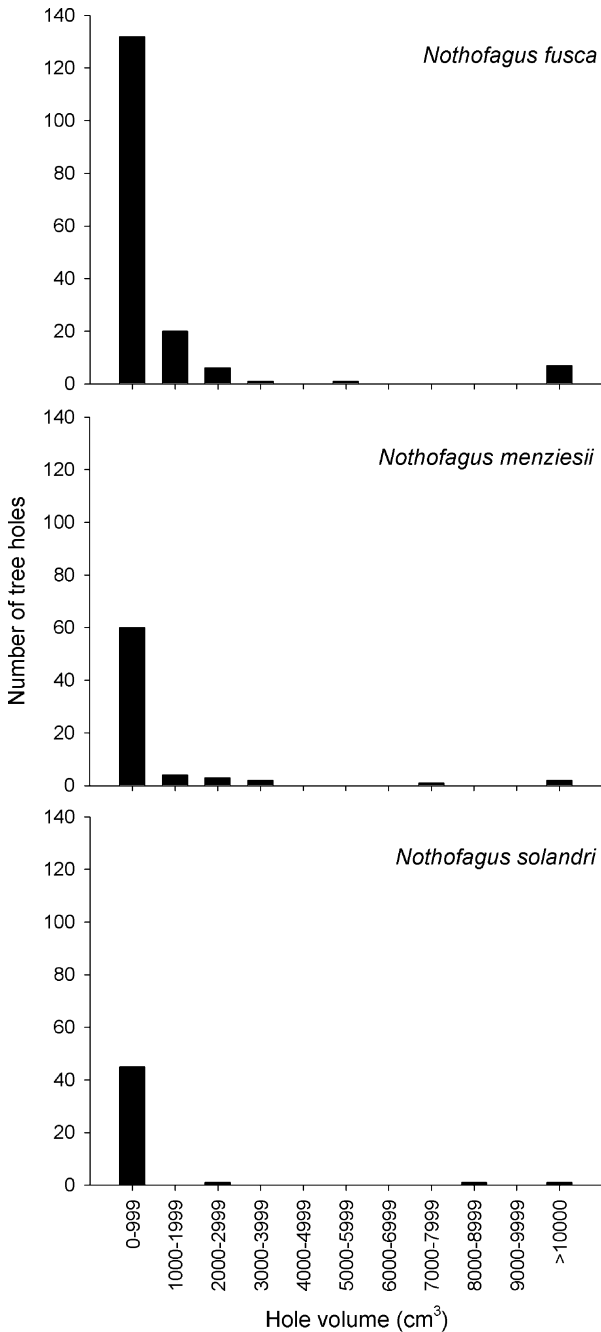


Fig. 2. The distribution of tree-hole volumes for 290 holes measured on ten *Nothofagus fusca*, *N. menziesii* and *N. solandri* during the direct, climbed inspections in the Lewis Pass National Reserve, April and September 2004.

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As expected from information gathered during the ground-based surveys, *N. fusca* had the greatest number of tree-holes in the climbed survey (ANCOVA, ln-transformed tree-hole count, species effect: $F_{2,24} = 4.15$, $P = 0.028$). More tree-holes were also found in large than small trees (ANCOVA, ln-transformed tree-hole count, d.b.h. effect: $F_{1,24} = 7.35$, $P = 0.012$; Fig. 3). However, in contrast to the ground-based surveys, there was no significant interaction between these two main effects, where the effect of tree size on tree-hole abundance was consistent across the three *Nothofagus* species (ANCOVA, ln-transformed tree-hole count, species \times d.b.h. interaction: $F_{2,24} = 3.30$, $P = 0.055$; Fig. 3). Of potentially greater interest was the fact that *N. fusca* also had the largest tree-holes. A mixed-effects GLM showed that there was a significant effect of tree species on hole volume ($F_{2,11.33} = 7.55$, $P = 0.008$), while the tree d.b.h. covariate also significantly affected hole volume ($F_{1,10.45} = 12.47$, $P = 0.005$; Table 2a). The effect of d.b.h. on tree-hole volume did not vary across the three tree species (species \times d.b.h. interaction: $F_{2,11.92} = 3.14$, $P = 0.08$), indicating that the increase in tree-hole volume with increasing tree size or age is consistent among these *Nothofagus* species (Fig. 4).

Unlike tree-hole volume, there was no significant effect of tree species on tree-hole entrance area (mixed-effects GLM, ln-transformed tree-hole entrance area, tree species main effect: $F_{2,10.30} = 2.13$, $P = 0.17$). Nevertheless, larger trees had tree-holes with substantially larger entrance areas ($F_{1,12.41} = 22.07$, $P < 0.001$;

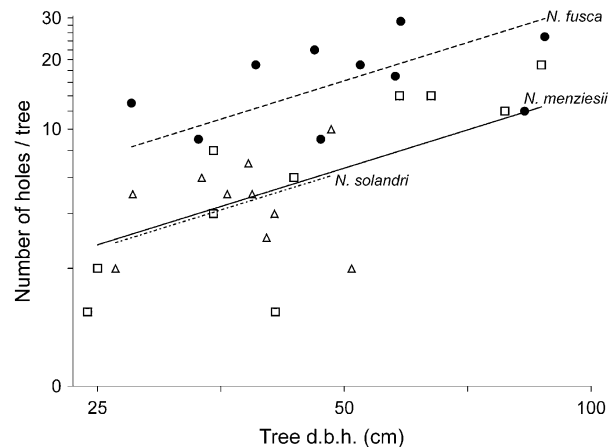


Fig. 3. Variation in the number of tree-holes recorded during climbed inspections of ten of each of *Nothofagus fusca* (closed circles and dashed fitted line), *N. menziesii* (open squares and solid fitted line) and *N. solandri* (open triangles and dash-dot fitted line) trees of differing sizes (d.b.h.) climbed in the Lewis Pass, April and September 2004. Note that the y-axis is plotted on a logarithmic scale. The equations of fitted lines are: $\ln(y) = -1.185 + 1.031 \cdot \ln(x)$ (for *N. fusca*), $\ln(y) = -1.999 + 1.031 \cdot \ln(x)$ (for *N. menziesii*) and $\ln(y) = -2.032 + 1.031 \cdot \ln(x)$ (for *N. solandri*).

Table 2. Mixed-effects generalized linear model analyses of variation in (a) tree-hole volume and (b) tree-hole entrance area on randomly selected *Nothofagus fusca* ($n = 10$), *N. menziesii* ($n = 9$) and *N. solandri* ($n = 10$) trees of differing sizes (diameter at breast height: d.b.h.)

Sources of variation	SS	d.f. effect	MS effect	d.f. error	MS error	F	P
(a) Tree-hole volume							
Tree species	120.48	2	60.24	11.33	7.98	7.55	0.008
Tree identity	45.07	9	5.01	8.55	9.62	0.52	0.826
Tree d.b.h.	101.78	1	101.78	10.45	8.16	12.47	0.005
d.b.h. × species	46.92	2	23.46	11.92	7.48	3.14	0.080
Tree identity × species	95.55	14	6.83	261.00	3.34	2.05	0.015
Error	871.15	261	3.34				
Total	1280.95	289					
(b) Tree-hole entrance surface area							
Tree species	13.54	2	6.77	10.30	3.17	2.13	0.167
Tree identity	11.92	9	1.32	7.55	3.87	0.34	0.933
Tree d.b.h.	65.30	1	65.30	12.41	2.96	22.07	0.001
d.b.h. × species	0.32	2	0.16	9.63	3.34	0.05	0.953
Tree identity × species	39.47	14	2.82	261.00	1.60	1.76	0.045
Error	418.85	261	1.61				
Total	549.40	289					

Only nine *N. menziesii* trees were included in the analyses as internal tree-hole dimensions were not able to be measured on of the one trees during the climbed inspections. Tree-hole volume and surface area were ln-transformed prior to analyses to normalize residuals. d.b.h. was ln-transformed and entered into the model as a fixed covariate. Tree identity was the random effect of variation in tree-hole size among individual trees within each tree species. Type-I sums of squares (SS) were used because of the hierarchical design of the treatments. Error degrees of freedom (d.f.) and error mean squares (MS) in F-ratio tests involving random treatment effects are calculated using the Satterthwaite (1946) method of denominator synthesis, which yields non-integer values. Significant P-values (≤ 0.050) are indicated in bold.

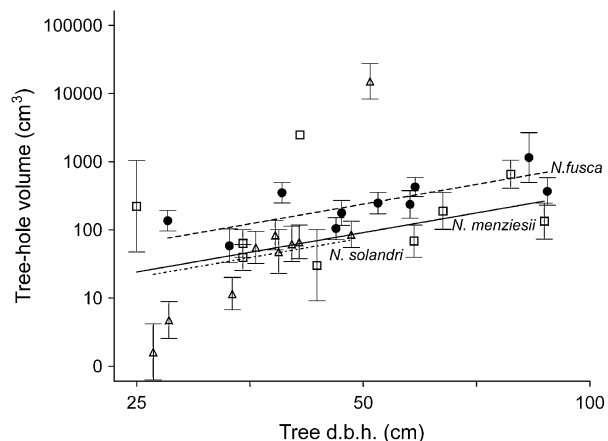


Fig. 4. Variation in the average (± 1 SE) tree-hole volume recorded on ten *Nothofagus fusca* (closed circles and dashed fitted line), nine *N. menziesii* (open squares and solid fitted line) and ten *N. solandri* (open triangles and dash-dot fitted line) trees of differing sizes (d.b.h.) climbed in the Lewis Pass, in April and September 2004. Note that the y-axis is plotted on a logarithmic scale. The equations of the fitted lines are: $\ln(y) = -2.037 + 1.920 \cdot \ln(x)$ (for hole volumes on *N. fusca*), $\ln(y) = -2.999 + 1.920 \cdot \ln(x)$ (for hole volumes on *N. menziesii*) and $\ln(y) = -3.178 + 1.924 \cdot \ln(x)$ (for hole volumes on *N. solandri*).

Table 2b). Again, the effect of d.b.h. did not vary across the three tree species (species × d.b.h. interaction: $F_{2,9.63} = 0.05$, $P = 0.95$), indicating that the increase in tree-hole entrance area with increasing tree size or age is consistent among these *Nothofagus* species.

Tree-holes were equally as common on N, E, S and W aspects ($\chi^2_{(6)} = 8.36$, $P = 0.213$). However, holes were slightly more common on trunks (182), than branches (104) ($\chi^2_{(2)} = 9.96$, $P = 0.012$), but this depended on tree species. *Nothofagus fusca* had half as many holes on branches (55) than trunks (110) and *N. solandri* showed a similar pattern (12 and 35, respectively). By contrast, holes were equally distributed on *N. menziesii*, with 37 holes located on both trunks and branches. Furthermore, several tree-hole characteristics were weakly, positively correlated with tree size (d.b.h.), including minimum internal dimensions ($r = 0.32$, $n = 290$, $P < 0.050$) and minimum entrance opening ($r = 0.32$, $n = 290$, $P < 0.05$). Holes situated higher above the forest floor also tended to have greater entrance areas ($r = 0.19$, $n = 290$, $P < 0.050$). However, of potentially greatest interest, hole entrance size was strongly, positively correlated with internal hole volume ($r = 0.62$, $n = 290$, $P < 0.001$). This was true for all three *Nothofagus* species, with larger tree-holes generally having greater entrance sizes on *N. fusca* ($r = 0.57$, $n = 168$, $P < 0.001$), *N. menziesii* ($r = 0.71$, $n = 73$, $P < 0.001$) and *N. solandri* ($r = 0.60$, $n = 49$, $P < 0.001$) (Fig. 5).

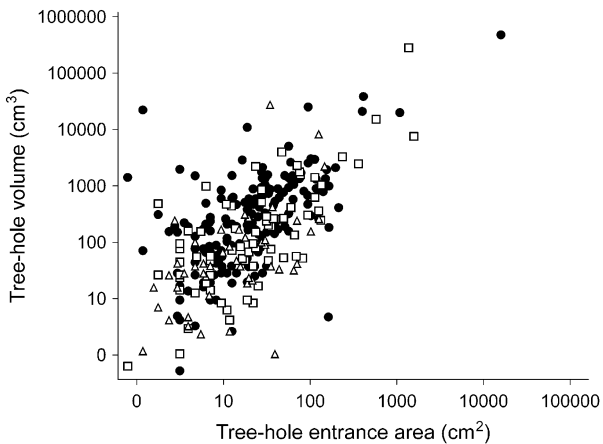


Fig. 5. The relationship between the entrance area (cm^2) of tree-holes and tree-hole volume (cm^3) for ten *Nothofagus fusca* (closed circles), nine *N. menziesii* (open squares) and ten *N. solandri* (open triangles) trees climbed in the Lewis Pass National Reserve.

Only 4% of all the tree-holes inspected contained standing water suitable for aquatic fauna to inhabit, while 27% were damp at the time of sampling. Thus, 31% of all holes contained some moisture (i.e. potentially containing water at times), while the remaining 69% of tree-holes were dry inside, in April (early autumn) or September (early spring) 2004. The majority (59%) of tree-holes faced downwards (negative entrance angle), yet entrance angle (positive angle, negative angle or 0°) was not a significant determinant of the internal conditions of these tree-holes (i.e. damp or dry) ($\chi^2_{(2)} = 0.28$, $P = 0.87$). Similarly, there were no clear relationships between internal dampness and tree species ($\chi^2_{(3)} = 3.30$, $P = 0.350$), hole aspect ($\chi^2_{(1)} = 0.50$, $P = 0.480$) or location on the tree ($\chi^2_{(2)} = 3.10$, $P = 0.210$). There were, however, significantly fewer water-filled or damp tree-holes on medium-sized (30.0–39.9 cm d.b.h.) *Nothofagus* trees than expected ($\chi^2_{(3)} = 9.80$, $P = 0.020$). Similarly, damp or water-filled tree-holes were more common (61%) than dry holes (39%), when an external lip was present at the entrance of the hole ($\chi^2_{(1)} = 7.50$, $P = 0.006$).

DISCUSSION

Formation, frequency and distribution of tree-holes

Despite the total absence of cavity-excavating woodpeckers and the relative paucity of large wood-boring insects in New Zealand, hole-bearing trees are abundant in unmodified *Nothofagus* forests (see also Elliott *et al.* 1996; Sedgley & O'Donnell 1999b). In comparison, hole-bearing trees overseas, such as Australian

Eucalyptus species and American beech (*Fagus grandifolia*) appear to have far fewer tree-holes than New Zealand's *Nothofagus* forests (Table 3). Abiotic processes leading to hole formation are important in both Australia and New Zealand, where tree-holes form when heartwood decay is present and a tree is exposed to some sort of physiological or physical stress (Gibbons & Lindenmayer 2002). However, the relative importance of different abiotic stressors is likely to be different in New Zealand, where disturbances from snow or wind storms are more important than fire. Furthermore, New Zealand has few hole-dwelling vertebrate species (approximately 14 native species) (Robertson 1985; Sedgley 2003), compared with the 303 Australian species that use holes for nesting, roosting, thermoregulation or feeding (Gibbons & Lindenmayer 2002). In Australia, parrots, cockatoos and arboreal marsupials are known to excavate both decayed and healthy wood, thereby assisting in hole formation (see review in Gibbons & Lindenmayer 2002). Thus, hole formation in Australian forest ecosystems is likely to be more similar to North America, where biotic factors, such as primary cavity-excavating fauna, strongly interact with abiotic disturbances in the hole formation process over time. Conversely, only a few of New Zealand's hole-dwelling birds, such as red-crowned kakariki (*Cyanoramphus novaezelandiae*) and kaka (*Nestor meridionalis*), are known to further excavate already established tree-holes (Greene 2003). Despite this, we found that tree-holes were extremely common in our study area. In fact, by extrapolating from the average number of holes found on climbed trees within each of four arbitrarily assigned size-classes (20–29.9, 30–39.9, 40–49.9, >50 cm d.b.h.), multiplied by the relative frequency of trees of that size present in the 0.36-ha study plot, we estimated that there might be as many as 3906 tree-holes per hectare of *Nothofagus* forest at this site. However, it is important to point out that tree-hole abundance was strongly dependent on both tree species and tree size, and is likely to vary to some degree between forest sites. These results are consistent with numerous studies of old-growth and second-growth forests in a range of other biogeographic regions, including the Midwestern USA (Fan *et al.* 2003) and Australia (Lindenmayer *et al.* 1993; Bennett *et al.* 1994; Gibbons *et al.* 2002; Whitford 2002; Harper *et al.* 2004).

In this study, climbed surveys revealed that *N. fusca* had on average many more holes than *N. menziesii* or *N. solandri* (Fig. 3). These findings may reflect differences in the properties of the timber and the associated susceptibility to rot and attack by decay-causing organisms (Stewart & Burrows 1994; Niemela *et al.* 1995; Allen *et al.* 2000; Olson 2003). Many insects, including tree weta *Hemideina* spp. and larvae of the moth *Heterocrossa eriphylla* almost certainly facilitate the development of rot in beech trees by keeping wounds open

Table 3. A comparison of the proportion of hole-bearing trees and mean number of holes per tree in the present study *versus* several studies overseas

Tree species	Country	No. trees in sample	Prop. hole-bearing	Holes/tree	Minimum entrance (cm)
<i>Nothofagus fusca</i>	NZ ¹	10	1.0 [†]	17.4	1.0
<i>Nothofagus menziesii</i>	NZ ¹	10	1.0 [†]	8.1	1.0
<i>Nothofagus solandri</i>	NZ ¹	10	1.0 [†]	4.9	1.0
<i>Nothofagus</i> spp.	NZ ²	78	0.2 [†]	0.7	1.7
<i>Nothofagus</i> spp.	NZ ³	120	0.6 [†]	0.3	1.7
<i>Acer saccharum</i>	USA ⁴	1201	0.2 [‡]	3.2	2.0
<i>Corymbia colaphylla</i>	Australia ⁵	40	0.5 [†]	1.9	2.0
<i>Eucalyptus leucoxylon</i>	Australia ⁶	40	0.9 [†]	7.8	1.0
<i>Eucalyptus marginata</i>	Australia ⁵	112	0.7 [†]	3.3	2.0
<i>Eucalyptus microcorys</i>	Australia ⁷	62	0.7 [‡]	–	1.0
<i>Eucalyptus pilularis</i>	Australia ⁷	111	0.5 [‡]	–	1.0
<i>Eucalyptus signata</i>	Australia ⁷	85	0.5 [‡]	–	1.0
<i>Fagus grandifolia</i>	USA ⁴	1489	0.2 [‡]	3.1	2.0
<i>Quercus</i> spp.	USA ⁴	2791	0.1 [‡]	4.1	2.0

¹This study; ²Sedgeley and O'Donnell (1999b); ³Sedgeley (2003); ⁴Fan *et al.* (2003); ⁵Whitford (2002); ⁶Harper *et al.* (2004); ⁷Wormington and Lamb (1999). [†]Indicates direct inspections (e.g. climbed inspections), while [‡]indicates ground-based surveys using binoculars.

to the air (Wardle 1967; Milligan 1974). Some beetles, such as the New Zealand native pinhole borer, *Platypus* spp., can also induce fungal attack and rotting, potentially playing an important role in tree-hole formation in *Nothofagus* forests (Wardle 1984). Interestingly, Litchwark (1978) found that *N. fusca* was 8–9 times more susceptible to *Platypus* attack than *N. menziesii*, which might partly explain why *N. fusca* had more tree-holes than the other beech species in this study. The variation in tree-hole abundance among species might also result from differential growth rates. For example, *N. menziesii* is typically slower growing than *N. solandri*, while *N. fusca* is the slowest growing *Nothofagus* species in New Zealand (Wardle 1984). Thus, in areas of equivalent site productivity, a *N. fusca* tree of a given diameter is likely to be older than a *N. solandri* or *N. menziesii* tree of the same size, and therefore might contain more holes due to age rather than size, *per se* (Lindenmayer *et al.* 1993; Bennett *et al.* 1994).

Nevertheless, tree-hole formation involves a complex set of processes that undoubtedly depends on many other factors such as stochastic events, genetic differences in rot susceptibility, and the chaotic nature of wind currents in the forest canopy (Robertson 1994). Therefore, it is not surprising that larger (and taller) trees not only had many more holes, but the holes were also bigger, both inside and outside. Research on Australian eucalypts suggests that although the propensity to develop tree-holes is dependant on tree species and size (Gibbons & Lindenmayer 2002), the matter is far more complicated. In fact, silvertop ash (*Eucalyptus sieberi*) is capable of occluding and shedding branches in response to mechanical wounding. By comparison, stringybark eucalypts retain, rather than shed, larger

branches. These persist when decayed, thereby increasing the susceptibility to hole formation (Gibbons & Lindenmayer 2002). There is also evidence of branch shedding in *N. menziesii* infected with the ascomycete fungi *Cyttaria*, where they cast off small branches before the fungus becomes properly established (Wardle 1984). Although these fungi are only known to attack *N. menziesii*, this selective branch shedding could provide some explanation for our findings of fewer tree-holes in *N. menziesii* than *N. fusca*.

Ground-based survey *versus* climbed tree inspections

Estimating the number of holes in trees or forest stands by counting visible holes from the ground is a widely used technique (Smith & Lindenmayer 1988; Lindenmayer *et al.* 1993; Bennett *et al.* 1994; Whitford 2002; Harper *et al.* 2004). However, tree-holes are difficult to see from the ground especially when they are vertically oriented with their openings in the fork of a tree, or on a branch. In this study, hole numbers were underestimated by the ground-based survey, compared with the climbed-tree inspections. Nevertheless, there was a significant correlation between the two techniques, with the climbed inspections consistently identifying almost four times more tree-holes than the ground surveys, regardless of tree size. Whitford (2002) found a similar relationship in Australia between the number of holes identified from the ground and entire trees surveyed post-harvesting for 211 jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees. He suggested that although the

correlation was significant, the coefficient was low ($r = 0.57$) and therefore the estimates produced from ground-based surveys were of little practical use (Whitford 2002).

Tree-holes high in the canopy and on branches can be the most difficult to detect from the ground (Whitford 2002). Our results highlight this, as only 18% of observable tree-holes were recorded on branches in the ground-based survey, compared with 38% from the climbed survey. Similarly, Harper *et al.* (2004) acknowledged that ground-based surveyors identified at most 44% of the total holes available in an Australian yellow gum (*Eucalyptus leucoxylon*) forest. Surprisingly, Sedgeley and O'Donnell (1999a) found no difference between ground-based and climbed-inspection counts in New Zealand *Nothofagus* forest. It is likely that this was because they only included cavities occurring on the main trunk and main lower limbs. In this study, ground surveyors identified, on average, 27% of total holes available on the 30 climbed *Nothofagus* trees. However, on one of the 30 climbed *Nothofagus* trees, 83% of all tree-holes were identified from the ground, while ten trees were recorded as having no holes even though it became clear that all trees had at least one hole when climbed. This provides further evidence for just how variable ground surveying can be. All the same, we agree with Harper *et al.* (2004) who concluded that the low proportion of holes identified should not rule out ground-based observations as an important method if they are used in conjunction with periodic climbed inspections to correct for bias. Instead, they argued that ground surveys are needed to show broad-scale spatial patterns within a study area, while the more intensive climbed surveys are necessary to provide essential information for the conservation of wildlife.

Implications for community structure and conservation

Tree-holes are an important ecological resource for forest communities, providing habitat for numerous vertebrate and invertebrate species worldwide (Elliott *et al.* 1996; Gibbons & Lindenmayer 2002; Ranius 2002). For example, the presence of standing water plays an integral role in determining the composition of tree-hole communities, supplying resources for highly specialized aquatic invertebrate communities (Kitching 1971). However, very little is known about water-filled tree-hole communities in New Zealand. In this study, more than 40% of all holes were facing upwards, and were therefore open to collecting rainwater, but despite this, less than 5% of tree-holes held standing water during our surveys. Although few tree-holes contained standing water, more than 30% were damp inside, indicating they may collect rainwater via stemflow at times. Despite the low proportion of

water-filled tree-holes encountered in this study, there may be as many as 120 holes per hectare that retain standing water for a period of time, providing important, albeit ephemeral resources for a multitude of aquatic and semi-aquatic invertebrate species (Kitching 1971; Yanoviak 2001; Taylor & Ewers 2003; T. J. Blakely, unpubl. data 2008).

Worldwide, many vertebrate species select holes with specific dimensions or characteristics for nesting and/or roosting in. For example, the entrance diameter and internal depth of a tree-hole are important characteristics for cockatoos in Western Australia (Saunders *et al.* 1982). Our findings show that large *Nothofagus* trees have many more, larger holes than smaller trees, particularly within large *N. fusca* trees. It is unsurprising therefore that many of New Zealand's hole-nesting bat and bird species, such as long-tailed bats, lesser short-tailed bats, mohua, yellow-crowned kakariki and rifleman (*Acanthisitta chloris*), preferentially select large *N. fusca* for roosting habitat over other *Nothofagus* species (Elliott *et al.* 1996; Sedgeley & O'Donnell 1999a; Sedgeley 2003). In fact, Sedgeley and O'Donnell (1999a) found that New Zealand's long-tailed and lesser short-tailed bats actively select large, tall trees with low canopy closure. Their preferred roosting holes are generally dry, situated more than 5 m above the ground and have very specific entrance and internal dimensions (minimum entrance dimensions 1.3×2.7 cm; volume 23 cm^3 ; Sedgeley & O'Donnell 1999b; Sedgeley 2003). In this study, most (90%) tree-holes measured were situated ≥ 5 m from the forest floor, and of those nearly 44% were dry and >59% were located on *N. fusca* trees. Moreover, 78 of the 290 tree-holes we measured on just 30 *Nothofagus* trees met all of the above criteria for bats (Sedgeley & O'Donnell 1999b; Sedgeley 2003), of which 67% were situated in *N. fusca*. Thus, our findings suggest that there could be as many as 963 holes per hectare that are suitable for long-tailed and lesser short-tailed bats in the *Nothofagus* forests of Lewis Pass National Reserve. This is very similar to a study in Fiordland National Park, where Sedgeley and O'Donnell (1999b) found 894 holes per hectare suitable as roost cavities for New Zealand's long-tailed bat.

Mohua and yellow-crowned kakariki also nest predominantly in holes of large *N. fusca* trees (Elliott *et al.* 1996). Of the numerous mohua and yellow-crowned kakariki nests Elliott *et al.* (1996) measured, both species generally used holes far from the forest floor (>14 m above ground), with average hole openings of 7.7 and 7.0 cm, respectively. At our study site, we found a very low proportion of tree-holes which fit all of these criteria for mohua and yellow-crowned kakariki, with an estimate of only eight holes per hectare. However, it is important to remember that this study was conducted in a relatively small area, so estimates such as these need to be treated with caution.

CONCLUSIONS

The formation of tree-holes is complex. The size and abundance of tree-holes changes with different growth stages of any given tree, which may in turn influence their use by hole-dwelling fauna (Lindenmayer *et al.* 1991). In this study, large *N. fusca* trees provided a large proportion of all tree-holes and more importantly, the majority of holes suitable for hole-dwelling fauna in New Zealand *Nothofagus* forests. This was consistent with other studies, where tree-hole abundance is influenced by both tree diameter and species (see review in Gibbons & Lindenmayer 2002). However, not all tree-holes were detectable from the ground, and as a result the absolute number of holes in a forest stand and their location within individual trees were greatly underestimated. Nevertheless, the degree to which tree-hole abundance was underestimated remained consistent with increasing tree size, thus ground-based surveys will be a useful technique in New Zealand *Nothofagus* forests when used in conjunction with climbed inspections.

Tree-holes were very abundant in the study area, and it is plausible that tree-holes are abundant in *Nothofagus* forests throughout much of New Zealand (e.g. Sedgley & O'Donnell 1999b), although larger-scale surveys need to be carried out to confirm this. Large holes suitable for some hole-nesting vertebrate species were also common in the study area. The majority of these were found in a few large trees, so hole frequency for vertebrates will be strongly dependant on stand dynamics and forest management practices that conserve large, hole-bearing trees. Nevertheless, small trees were very common in the study area, contributing proportionally more tree-holes than large trees, and should not be overlooked in forest management practises. Finally, this is the first systematic survey of the distribution and structural characteristics of tree-holes in New Zealand and provides an ideal framework for future research on how structural characteristics, spatial patchiness and ephemerality of resources may affect species composition and community structure.

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