

The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada

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Abstract Nest-holes created by woodpeckers or natural decay processes are an essential commodity for secondary hole-nesting species. Hole-making agents may strongly influence the richness and abundance of species in hole-nester communities. However, few studies have examined the characteristics and relative importance of naturally occurring holes for hole-nesters. Between 1995 and 2006, we examined 1371 excavated and non-excavated holes used by 29 bird and mammal species in central British Columbia, Canada. Excavated holes were much more abundant (85%) than non-excavated holes (15%). Red-naped sapsucker (*Sphyrapicus nuchalis*) and northern flicker (*Colaptes auratus*) excavated 52% of the holes monitored. At the community level, non-excavated holes were used for nesting less than expected based on their availability (6% of total nests), particularly among woodpeckers (2% of nests). However, secondary hole-nesters used non-excavated holes roughly in proportion to their availability (10% of nests), and some excavators used non-excavated holes for nesting (flicker and red-breasted nuthatch, *Sitta canadensis*, 4% of nests each; black-capped chickadee, *Poecile atricapillus*, 13% of nests). Although nests in non-excavated holes tended to be lower on the tree,

larger internally and with larger entrances, only European starling (*Sturnus vulgaris*) appeared to select non-excavated holes with characteristics most similar to their preferred excavated holes. Non-excavated holes may be an alternate nesting resource for secondary hole-nesters that cannot acquire an excavated hole and, occasionally, for excavators. The use of non-excavated holes may provide an advantage for secondary hole-nesters by releasing them from the constraints of excavator nest-site preferences.

Keywords Hole-nesting birds and mammals · Importance of excavators · Keystone excavators · Natural holes · Secondary hole-nesters

Introduction

A broad range of bird, mammal, reptile, amphibian and insect species worldwide use holes in trees for nesting, roosting, food storage and cover, including over 100 bird and mammal species in North America (Burt and Grossenheider 1980; Newton 1998). Tree holes provide secure sites from predators and inclement weather, and their availability and distribution are considered to shape life history traits and community structure for the group (Martin 1993; Martin et al. 2004; Wiebe et al. 2006). Excavators such as woodpeckers create holes in dying or dead wood. Non-excavated holes may originate from broken tree limbs, crevices behind bark, hollow stumps, wound openings and a range of fungal and other decay processes. Holes may remain in the landscape for several years to decades, providing a required nesting resource for non-excavating secondary hole-nesters and an option for excavators to reuse existing holes (Aitken et al. 2002; Wiebe et al. 2006).

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Researchers have recently begun to examine the relative importance of excavated versus non-excavated holes. Woodpeckers are considered to be keystone species in many systems because, by providing nest-sites for secondary hole-nesters, they may influence the abundance and distribution of other species in the community (Daily et al. 1993; Martin and Eadie 1999). However, in some systems non-excavated holes may be plentiful enough that excavated holes are used relatively infrequently or are avoided by secondary hole-nesters (Carlson et al. 1998; Remm et al. 2006; Wesolowski, this issue). Non-excavated holes may also be less susceptible to predation by large woodpecker species than excavated holes (Walankiewicz 2002; Wesolowski 2002). However, few studies have examined differences between excavated and non-excavated holes (Bai et al. 2003). In many studies of nest-site selection, hole origin is not recorded. Comparing the use and availability of excavated and non-excavated holes may provide insight into the importance of woodpeckers as keystone species and into the nest-site requirements of secondary hole-nesters when they are released from the constraints of woodpecker nest-site preferences and, potentially, competition for excavated holes.

The hole-nesting bird and mammal community of Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests of central British Columbia, Canada is one of the richest in North America (Martin and Eadie 1999). Approximately 22% of the bird species in the region are hole-nesters, and both excavators and non-excavators use non-excavated holes (Martin and Eadie 1999; Aitken and Martin 2004). In this paper, we examine the use of excavated and non-excavated holes by excavators and secondary hole-nesters and compare characteristics of excavated and non-excavated holes used for nesting at the community level, and by several individual species. We also consider hole type in relation to forest context and present the results of a survey of availability of excavated and non-excavated holes.

Methods

Study area

Between 1995 and 2006, we located holes and monitored nests of hole-nesting birds and mammals on our study area in the Cariboo-Chilcotin region of central interior British Columbia (51°52'N, 122°21'W). In 1995, we established 11 sampling sites, increased this to 16 sites in 1996, and since 1998 we have monitored 28 sites. The study area was composed of mixed coniferous and deciduous forest embedded in a matrix of grassland and shallow ponds. Predominant tree species were lodgepole pine (*Pinus*

contorta), Douglas-fir, trembling aspen (*Populus tremuloides*) and hybrid white-Engelmann spruce (*P. glauca* × *engelmannii*). Our sampling sites (7–32 ha in size) varied in character from continuous forest (26 sites) to two sites that were a series of mature aspen–conifer groves (0.2–5 ha) within a grassland matrix. Fifteen of the continuous forest sites were mature (80–200 years old) mixed conifer forest, nine were selectively cut for pine or spruce in 1997–2002, and two were selectively logged for Douglas-fir in the 1940s. Additional details for the study area and project design are given in Aitken and Martin (2004) and Martin et al. (2004).

Nest location and monitoring

From 1 May to 31 July 1995–2006, all sites were searched for occupied hole-nests. In our study area, most migratory and resident hole-nesters did not begin nesting until the first or second week of May. Systematic nest searches were conducted across all sites for an average of 6–7 observer-hours of nest searching per sampling site per week. Because hole-nesters reused holes and nest-trees in multiple years (Aitken et al. 2002), both existing holes (both previously used and those not known to be occupied in previous years) and newly excavated holes were checked.

Occupied holes were located by looking or listening for excavation, by tapping or scraping at the base of trees containing holes to detect occupants and by observing breeding birds or hearing begging nestlings. Finding occupied nests was facilitated by detecting general locations of hole-nesters during early morning point-count surveys. Holes within reach of a ladder (≤5.2 m) were inspected visually with flashlights and mirrors. In 2005 and 2006, a TreeTop Peeper camera system (Sandpiper Technologies, Manteca, Calif.) was used to monitor holes up to 17 m off the ground and in trees too unstable to reach with a ladder. Nests were considered occupied if they contained at least one egg or nestling. We also monitored holes occupied by hole-nesting mammals such as red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*) and bushy-tailed woodrat (*Neotoma cinerea*) as well as use by facultative hole users such as deer mouse (*Peromyscus maniculatus*), short-tailed weasel (*Mustela erminea*), fisher (*Martes pennanti*) and chipmunk (*Eutamias* spp.). Occupied holes were assigned unique numbers, and nest trees were marked with numbered aluminum tags to facilitate relocation across the study years.

Nest tree and hole characteristics

After nest-holes were vacated, we recorded tree and hole variables. Hole origin was categorized as excavated or non-excavated. Because non-excavated holes were located in

broken branch nodes, behind bark, tops of stumps, among others, these were clearly distinguishable from excavated holes. Species of the hole excavator was recorded if observed during excavation or if determination was possible from diagnostic features, such as entrance size and shape. Tree characteristics recorded included species, decay stage (live or dead) and diameter at breast height (DBH). Hole variables included height above ground (m), vertical depth (cm), internal diameter (cm), entrance height and width (cm) and orientation. Vertical depth was measured from the bottom of the hole entrance to the floor of the hole. Internal diameter was measured from the inner edge of the lower lip of the entrance to the back wall of the hole. Entrance area (cm²) was calculated using entrance height and width and the formula for the area of an ellipse. Distance to nearest forest edge (grassland, pond or stream) was recorded either directly using 30 m measuring tapes or by Global Positioning System (GPS).

Availability of excavated and non-excavated holes

In 2000, we surveyed hole availability in five continuous forest sites, and in 35 aspen groves (0.05–3 ha). At each continuous forest site, we established three transect lines, 100 m apart, starting at the forest edge and extending 350 m into the forest. Walking along each transect, we recorded all holes within 10 m on either side of the line. In each grove, we searched throughout the entire patch, recording all holes. The same two observers surveyed each site to ensure that hole-searching techniques were consistent among sites. We did not include partially excavated trial holes in our surveys, nor holes with a vertical depth of <1 cm. We recorded tree and hole characteristics as described above for nest-holes.

Data analyses

We used linear mixed effects (LME) models to determine whether tree and hole characteristics differed among nests in excavated and non-excavated holes. The nest-site variables examined were height above ground, vertical depth, internal diameter, entrance area, tree DBH and distance from grove or forest edge. Data were analyzed using the procedure LME in the statistical program R ver. 2.4.0 (R Development Core Team 2006). We built separate models for each nest-site variable. Each model included the dependent variable of interest (e.g. height above ground) and hole type (excavated or non-excavated) as the fixed effect. Because holes were used multiple times across years, we included individual hole as a random effect in each model. Distance to edge followed a Poisson distribution in continuous forest sites; thus, we used generalized linear mixed models with a penalized quasi-likelihood

method of parameter estimation (GLMMPQL; Breslow and Clayton 1993; Nelson and Leroux 2006) to compare distance to edge among excavated and non-excavated holes in those sites. PQL is an approximate method of inference in GLMMs in which maximum likelihood methods are not appropriate due to the distribution of random effects (Wedderburn 1974; Breslow 2003). Independent samples *t*-tests were used to compare characteristics of excavated and non-excavated holes recorded in our hole availability survey. Where necessary, data were log- or square-root transformed in order to meet assumptions of normality and equality of variance. Where data could not be transformed to meet assumptions, non-parametric Mann–Whitney *U*-tests were used. We tested whether the orientation of the excavated and non-excavated hole entrances was random or non-random using one-sample Watson’s *U*²-tests for circular distributions, and mean orientation of excavated and non-excavated holes were compared using two-sample Watson’s *U*²-test in the statistical program ORIANA ver. 2.0.2 (Kovach Computing Services 2005). Chi-square tests were used to compare the proportions of excavated and non-excavated holes in continuous forests versus aspen groves, and in live versus dead trees.

Results

Excavated versus non-excavated holes used for nesting

We were able to identify the mode of creation (excavated or non-excavated) for 1371 individual holes used for nesting in 1057 trees on our study sites between 1995 and 2006. Of these holes, 95% were excavated and 5% were non-excavated. Red-naped sapsucker (*Sphyrapicus nuchalis*) and northern flicker (*Colaptes auratus*) excavated 52% of all holes, 19% were excavated by other woodpecker species and 11% were excavated by chickadees (*Poecile* spp.) or red-breasted nuthatch (*Sitta canadensis*; Table 1). Among non-excavated holes, most were in broken branch nodes, crevices behind loose bark and hollow stumps (“chimneys”). Two unusual mountain bluebird (*Sialia currucoides*) nests (one wedged in a cracked boulder, the other in the hollow end of a metal bridge piece) were not included in our analyses of non-excavated holes.

We monitored 2728 nesting attempts, 94% of which were in excavated holes and 6% in non-excavated holes. As expected, the proportion of nests in non-excavated holes differed among excavators and secondary hole-nesters, with 10% of secondary hole-nester nests in non-excavated holes and just 2% of excavator nests in non-excavated holes. While northern flicker was the only woodpecker that used both excavated and non-excavated holes, only 4% of flicker nests were in non-excavated holes (Table 1). The

Table 1 Bird and mammal species nesting in excavated and non-excavated tree holes and the percentage of total holes excavated by woodpecker and other excavator species in Interior British Columbia, Canada, 1995–2006

Scientific name	Common name	Percentage of nests in excavated holes	Percentage of nests in non-excavated holes	Total nests	Percentage of holes excavated (n = 1371)
Excavators					
<i>Sphyrapicus nuchalis</i>	Red-naped sapsucker	100	0	372	31
<i>Sphyrapicus ruber</i>	Red-breasted sapsucker	100	0	2	1
<i>Picoides pubescens</i>	Downy woodpecker	100	0	63	5
<i>Picoides villosus</i>	Hairy woodpecker	100	0	74	6
<i>Picoides dorsalis</i>	American three-toed woodpecker	100	0	56	4
<i>Picoides arcticus</i>	Black-backed woodpecker	100	0	4	2
<i>Colaptes auratus</i>	Northern flicker	96	4	407	21
<i>Dryocopus pileatus</i>	Pileated woodpecker	100	0	31	3
<i>Poecile atricapillus</i>	Black-capped chickadee	87	13	38	2
<i>Sitta canadensis</i>	Red-breasted nuthatch	96	4	243	9
	Unknown excavator	NA	NA	NA	13
Total excavators		98	2	1290	
Secondary hole-nesting birds (SHN)					
<i>Aix sponsa</i>	Wood duck	100	0	1	
<i>Bucephala albeola</i>	Bufflehead	97	3	58	
<i>Bucephala islandica</i>	Barrow's goldeneye	100	0	5	
<i>Lophodytes cucullatus</i>	Hooded merganser	100	0	1	
<i>Falco sparverius</i>	American kestrel	95	5	42	
<i>Otus flammeolus</i>	Flammulated owl	100	0	1	
<i>Surnia ulula</i>	Northern hawk owl	0	100	2	
<i>Aegolius acadicus</i>	Northern saw-whet owl	100	0	17	
<i>Tachycineta bicolor</i>	Tree swallow	91	9	307	
<i>Poecile gambeli</i>	Mountain chickadee	93	7	295	1 ^a
<i>Sialia currucoides</i>	Mountain bluebird	86	14	253	
<i>Sturnus vulgaris</i>	European starling	89	11	341	
	Unidentified SHN	67	33	3	
Total SHN		90	10	1326	
Small mammals					
<i>Glaucomys sabrinus</i>	Northern flying squirrel	86	14	14	
<i>Tamias</i> spp.	Chipmunk	0	100	2	
<i>Tamiasciurus hudsonicus</i>	Red squirrel	90	10	81	
<i>Neotoma cinerea</i>	Bushy-tailed woodrat	67	33	6	
<i>Peromyscus maniculatus</i>	Deer mouse	100	0	1	
<i>Martes pennanti</i>	Fisher	100	0	1	
<i>Mustela erminea</i>	Short-tailed weasel (ermine)	100	0	1	
	Unidentified small mammal	100	0	2	
Total small mammals		87	13	108	
Bark nesters					
<i>Certhia americana</i>	Brown creeper	0	100	4	

^a Two holes were excavated by mountain chickadee, which we classify as a SHN as per Hill and Lein (1988)

only species that used non-excavated holes more than 20% of the time was the bushy-tailed woodrat (Table 1).

With all species grouped together, nests in excavated holes were on average almost 2 m higher above ground

than nests in non-excavated holes (Fig. 1a, Table 2). Excavated holes used for nesting were significantly narrower internally (Fig. 1c) and had smaller entrances than non-excavated holes (Fig. 1d, Table 2). Vertical hole depth

and tree DBH did not differ among excavated and non-excavated holes used for nesting when all species were grouped (Fig. 1b, e, Table 2). While there was little difference in distance to the nearest edge among nests in excavated and non-excavated holes in aspen groves, nests in excavated holes in continuous forest were farther from the edge than those in non-excavated holes (Fig. 2). However, this was not significant in our mixed model analysis (Table 2). Orientations of excavated and non-excavated holes were non-random, with more holes facing southeast than other directions (Watson’s one-sample U^2 -test; excavated holes: $\mu = 211 \pm 100^\circ$, $U^2 = 3.1$, $n = 1289$, $p < 0.005$; non-excavated holes: $\mu = 203 \pm 99^\circ$, $U^2 = 0.2$, $n = 64$, $p < 0.05$; Fig. 3). Mean orientation did not differ between excavated and non-excavated holes (Watson’s two-sample U^2 test: $U^2 = 0.07$, $p > 0.05$, $n = 1289$, 64).

Five species had large enough sample sizes to allow us to compare the characteristics of nests in excavated and non-excavated holes: northern flicker, mountain chickadee

(*Poecile gambeli*), mountain bluebird, European starling (*Sturnus vulgaris*) and tree swallow (*Tachycineta bicolor*). Northern flicker nests (which averaged 2.8/ha in our study sites) in excavated holes were significantly higher above ground and shallower than those in non-excavated holes (Fig. 1, Table 2). Mountain chickadee nests (mean: 0.7 nests/ha) in excavated holes were significantly shallower than those in non-excavated holes (Fig. 1, Table 2). In continuous forests, mountain chickadee nests in excavated holes were significantly farther from the edge than were nests in non-excavated holes (Fig. 2, Table 2). This trend was reversed in aspen groves, where mountain chickadee nests in non-excavated holes were more than twice as far from the edge as were those in excavated holes (Fig. 2, Table 2). Of the five species examined, only mountain chickadees nested in both excavated and non-excavated holes in continuous forest sites (Fig. 2). Mountain bluebird nests (mean: 2.8 nests/ha) in excavated holes were significantly higher above ground, had considerably smaller entrances and were in smaller trees than those in

Fig. 1 Characteristics of excavated and non-excavated holes used by all species (“Total nests”) and by five individual species. See Table 1 for full species names and Table 2 for results of mixed models analyses

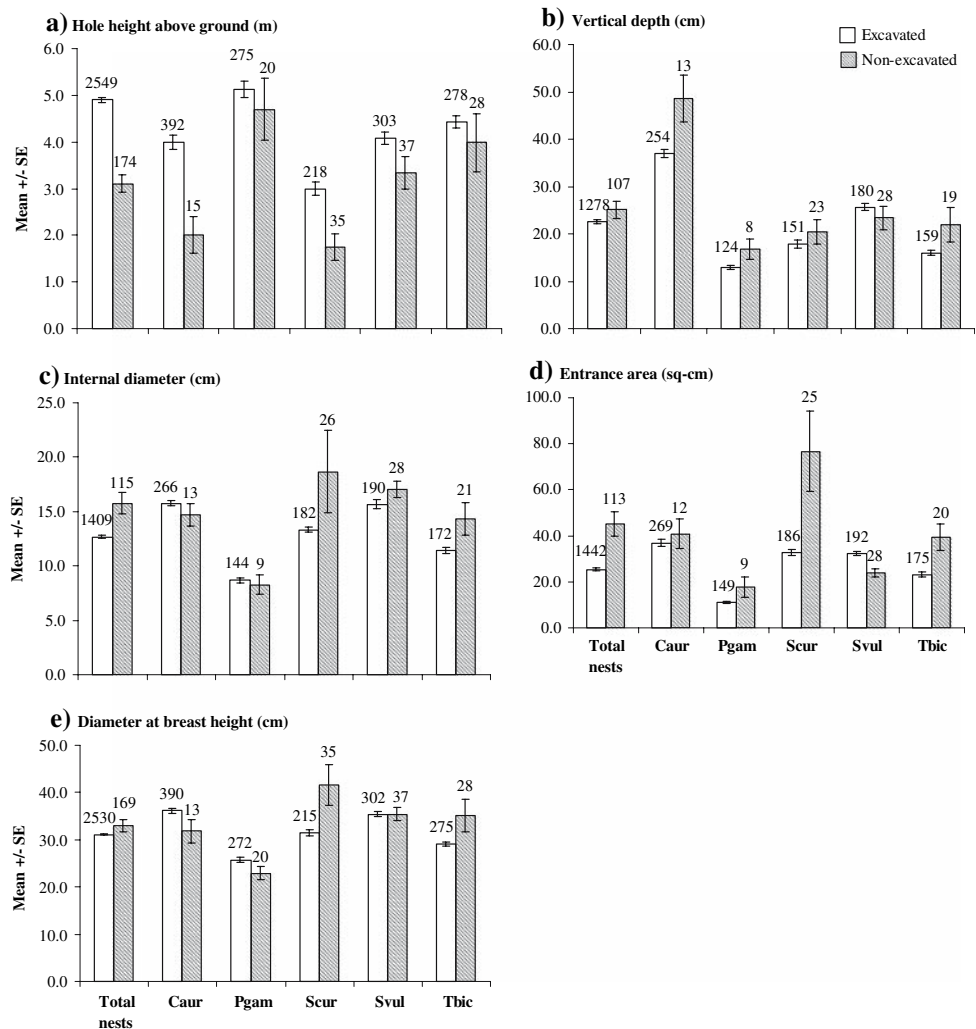


Table 2 Linear mixed effects models predicting nest-site characteristics of hole-nesting birds and mammals in Interior British Columbia, Canada, between 1995 and 2006 (DBH diameter at breast height)

Species	Estimate (excavated vs. non-excavated)	Standard error	df	t	p
<i>All species</i>					
Hole height above ground (m) ^a	-0.61	0.08	1364	-7.44	<0.0001
Vertical depth (cm) ^a	0.23	0.20	664	1.15	0.25
Internal diameter (cm) ^b	0.22	0.06	702	3.78	0.0002
Entrance area (cm ²) ^b	0.51	0.10	709	4.95	<0.0001
Tree DBH (cm) ^b	0.003	0.01	1653	0.24	0.81
Distance to nearest edge (groves) ^a	-0.15	0.27	438	-0.55	0.58
Distance to nearest edge (continuous forest) ^c	0.005	0.49	704	0.01	0.99
<i>Colaptes auratus</i>					
Hole height above ground (m) ^b	-0.52	0.24	239	-2.14	0.03
Vertical depth (cm) ^b	0.30	0.13	155	2.35	0.02
Internal diameter (cm) ^b	-0.08	0.08	160	-0.90	0.37
Entrance area (cm ²) ^b	-0.01	0.10	159	-0.13	0.90
Tree DBH (cm) ^b	-0.08	0.10	237	-0.72	0.47
Distance to nearest edge (groves) ^a	0.26	0.61	139	0.42	0.68
<i>Poecile gambeli</i>					
Hole height above ground (m)	0.32	0.93	186	0.34	0.73
Vertical depth (cm)	3.89	1.67	88	2.33	0.02
Internal diameter (cm) ^b	-0.12	0.17	99	-0.7	0.48
Entrance area (cm ²) ^b	0.04	0.22	100	0.17	0.87
Tree DBH (cm) ^b	-1.04	2.30	184	-0.45	0.65
Distance to nearest edge (groves)	24.0	8.37	23	2.86	0.009
Distance to nearest edge (continuous forest) ^c	-1.55	0.78	124	-1.98	0.05
<i>Sialia currucoides</i>					
Hole height above ground (m)	-1.64	0.65	140	-2.53	0.01
Vertical depth (cm) ^a	0.42	0.40	101	1.06	0.29
Internal diameter (cm)	1.48	1.03	108	1.44	0.15
Entrance area (cm ²) ^b	0.34	0.18	111	1.94	0.06
Tree DBH (cm) ^b	0.20	0.09	137	2.27	0.02
Distance to nearest edge (groves) ^a	0.02	0.48	100	0.05	0.96
<i>Sturnus vulgaris</i>					
Hole height above ground (m) ^b	-0.24	0.20	131	-1.21	0.23
Vertical depth (cm) ^b	-0.14	0.11	90	-1.24	0.22
Internal diameter (cm) ^b	0.15	0.10	93	1.47	0.15
Entrance area (cm ²) ^b	-0.37	0.12	93	-3.01	0.003
Tree DBH (cm) ^b	0.007	0.09	131	0.08	0.94
Distance to nearest edge (groves)	1.24	2.72	108	0.46	0.65
<i>Tachycineta bicolor</i>					
Hole height above ground (m) ^b	-0.31	0.15	201	-2.15	0.03
Vertical depth (cm) ^a	0.49	0.32	118	1.52	0.13
Internal diameter (cm) ^b	0.20	0.09	128	2.18	0.03
Entrance area (cm ²) ^b	0.55	0.16	128	3.40	0.0009
Tree DBH (cm) ^b	0.12	0.07	199	1.76	0.08
Distance to nearest edge (groves) ^b	0.07	0.46	122	0.15	0.88

Separate models were built for each of six nest-site characteristics, with hole type (“excavated”, “non-excavated”) as the fixed effect, and individual hole as the random effect. A positive estimate indicates that excavated holes had a higher mean value than non-excavated holes, and vice versa for negative estimates

^a Square-root transformed data used in analysis

^b Log-transformed data used in analysis

^c Analysis using generalized linear mixed models, with penalized quasi-likelihood parameter estimation (GLMMPQL; see text for further explanation)

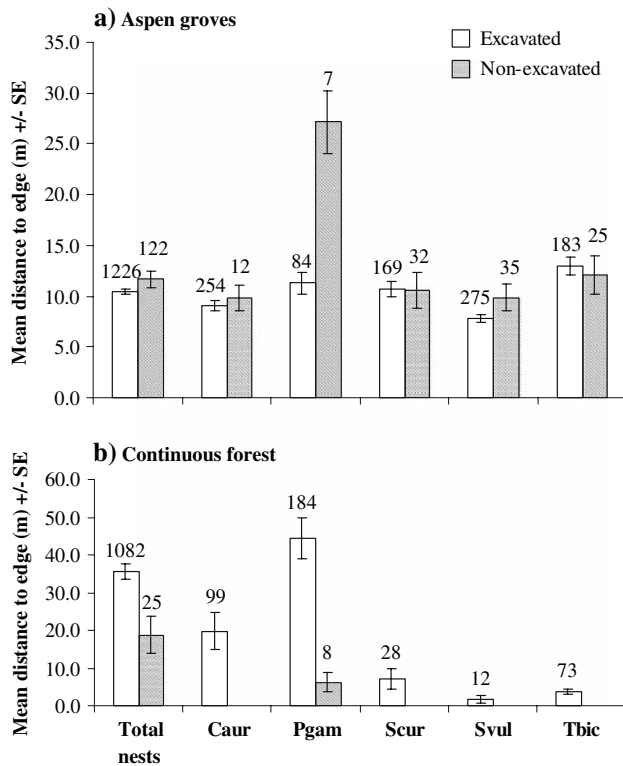


Fig. 2 Distance of nests in excavated and non-excavated holes to the nearest edge in aspen groves and in continuous forest sites. See Table 1 for full species names, and Table 2 for results of mixed models analyses

non-excavated holes (Fig. 1, Table 2). There were few differences between excavated and non-excavated holes used by European starling (mean: 5 nests/ha), although the entrance areas of excavated starling nests were significantly larger than those of non-excavated holes (Fig. 1, Table 2). Tree swallow nests (mean: 2.4 nests/ha) in excavated holes were significantly higher above ground, narrower internally and had smaller entrances than nests in non-excavated holes (Fig. 1, Table 2).

Availability of excavated versus non-excavated holes

In 2000, we surveyed 200 available holes, of which 85% were excavated and 15% were non-excavated. The mean density of excavated holes was 11.2 per hectare versus 1.1 per hectare for non-excavated holes. Aspen groves had a slightly lower proportion of non-excavated holes than continuous forests (14% of 180 holes in groves, 20% of 20 holes in continuous forests), but this difference was not significant ($X^2 = 0.44$, $df = 1$, $n = 200$, $p = 0.5$). While non-excavated holes were similar to excavated holes in terms of height above ground, internal diameter and distance to nearest edge, they tended to be deeper and have larger entrances, but not significantly so (Table 3). Trees

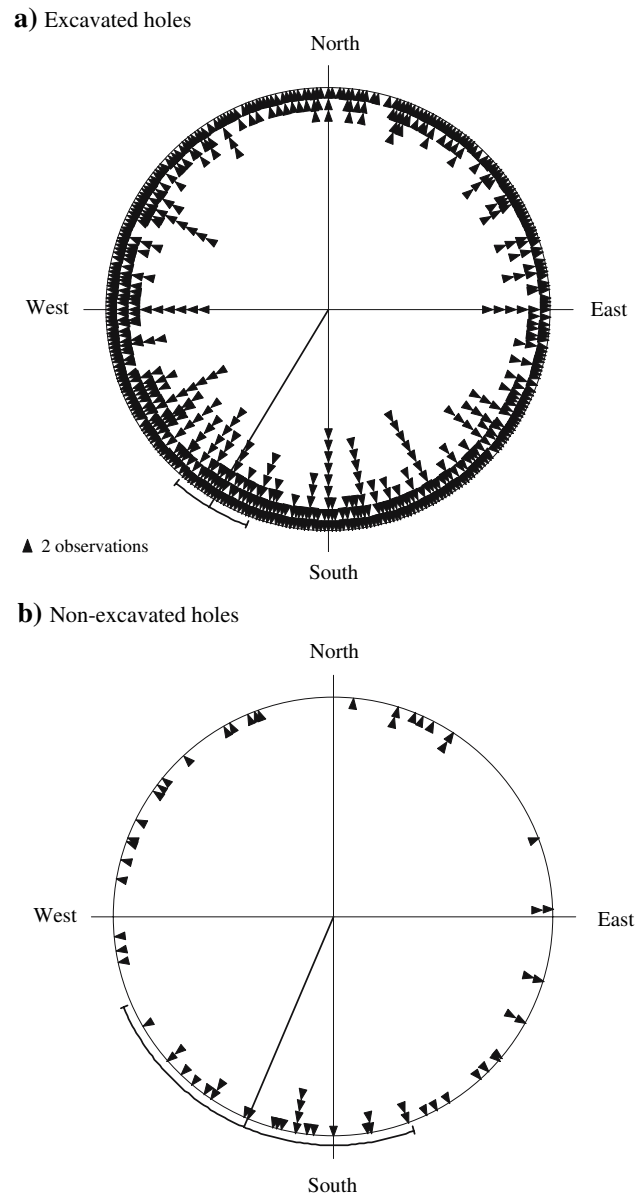


Fig. 3 Orientation of excavated (a) and non-excavated holes (b). The arrow indicates mean orientation and the arcs to either side indicate the 95% confidence interval. See text for results of statistical tests

with excavated holes did not differ in stage of decay from those with non-excavated holes (Live versus dead: $X^2 = 0.02$, $df = 1$, $n = 200$, $p = 0.9$).

Discussion

Both the availability and use of excavated and non-excavated holes vary across forest types and ages, landscape types and, possibly, continents (Wesołowski, this issue). Costs and benefits associated with hole origin as well as competitive abilities to secure a preferred hole type may

Table 3 Characteristics of available excavated and non-excavated holes surveyed in continuous forests and aspen groves in 2000

Variable	mean \pm SE		Test statistic ^a	df	p
	Excavated	Non-excavated			
Hole ht above ground (m)	2.7 \pm 0.1	2.7 \pm 0.2	-0.29	198	0.8
Vertical depth (cm) ^b	24.4 \pm 1.8	31.8 \pm 6.9	-1.29	172	0.2
Internal diameter (cm)	13.2 \pm 0.4	12.8 \pm 1.1	0.40	180	0.7
Entrance area (cm ²) ^c	25.2 \pm 1.0	38.2 \pm 7.4	-1.20	178	0.2
Diameter at breast height (cm) ^b	34.2 \pm 0.9	33.5 \pm 3.1	1.30	197	0.2
Nearest edge (m)	25.7 \pm 4.2	22.0 \pm 7.4	2520.5	198	0.9

^a Mann–Whitney *U*-test for nearest edge; independent samples *t*-test for all others

^b Log-transformed data used in analysis

^c Square-root transformed data used in analysis

vary among species. Here, we discuss the variation in abundance and use of the two major hole types across species and in relation to forest type and context for northwestern North America.

Previous studies in forests of Europe and Asia reported a wide range in the relative abundance of excavated and non-excavated holes. Remm et al. (2006) found that woodpeckers excavated 88% of holes in deciduous forests in Estonia, while Carlson et al. (1998) found that 47% of holes in Swedish deciduous forest were excavated. In contrast, in primeval mixed forests in eastern Poland, non-excavated holes were much more abundant than excavated holes (11–11.5 vs. 4.5–5 holes/ha), and 85% of secondary hole-nesters nested in non-excavated holes (Wesołowski, this issue). In Mongolian mature forests, 75% of nesting attempts were in non-excavated holes (Bai et al. 2003). On our study sites, excavated holes were much more abundant (11.2 holes/ha) than non-excavated holes (1.1/ha). Woodpeckers were abundant in our region, and individuals may excavate multiple holes each year (Bonar 2000; Walters et al. 2002). Because these holes are often excavated in live trees or those in the earliest stages of decay, these holes may persist for several years to over 30 years (Aitken et al. 2002; Wesołowski, this issue). If excavated holes are created at a faster rate than non-excavated holes or survive longer, this may lead to a greater supply of excavated holes compared to non-excavated holes in the landscape.

While secondary hole-nesters as a group used excavated and non-excavated holes approximately in proportion to their availability in the landscape, the use of non-excavated holes varied among species. The larger secondary hole-nester species, bufflehead (*Bucephala albeola*), Barrow's goldeneye (*Bucephala islandica*), American kestrel (*Falco*

sparverius) and northern saw-whet owl (*Aegolius acadicus*) used non-excavated holes less frequently than some of the smaller secondary hole-nesters, such as bluebird and starling. Although non-excavated holes tended to be larger on average than excavated holes, these holes were also relatively scarce. Therefore, large-bodied hole-nesters may be constrained by the availability of large holes and rely primarily on those created by large excavators (Martin et al. 2004).

There were ten excavating species in our study region, including 10- to 11-g chickadee and nuthatch, and eight species of woodpecker ranging in mass from the 30-g downy woodpecker (*Picoides pubescens*) to the 300-g pileated woodpecker (*Dryocopus pileatus*; Campbell et al. 1990; Bull and Jackson 1995; Martin and Norris 2007). This excavator group provides holes across a broad range of habitat types that accommodate an array of secondary hole-nesters from 10-g chickadees to 1-kg Barrow's goldeneye and 2.5-kg fisher (Martin et al. 2006). In European forests, woodpecker species diversity was positively correlated with secondary hole-nester diversity, likely due to an increase in hole diversity in stands with a variety of woodpeckers (Mikusiński and Angelstam 1998). With a broad range of excavating species in the community and, thus, a wide variety of potential nest-sites available, secondary hole-nesters may not be as dependent on non-excavated holes as in systems in which the excavator assemblage has been altered.

Three excavators, northern flicker, red-breasted nuthatch, and black-capped chickadee (*Poecile atricapillus*), used a small proportion of non-excavated holes for nesting in our sites. Nuthatches and chickadees are weak excavators that require trees in advanced stages of decay for excavation, and they may be limited by the availability of these trees (Dickson et al. 1983; Steeger and Hitchcock 1998). Naturally occurring holes may provide ready-made nest-sites when suitable trees are unavailable for excavation for these species. The only woodpecker to use non-excavated holes in our study, northern flicker, experiences aggressive competition from European starlings and is often evicted from its nest holes (Moore 1995; Wiebe 2003). The use of non-excavated holes may be a means to avoid competition from starlings and other secondary hole-nesters and may allow excavators to initiate breeding earlier (Wiebe et al. 2006).

Non-excavated holes used for nesting tended to be larger internally and had larger entrances than excavated holes. Both hole entrance size and internal size have been linked with fecundity and reproductive success in hole-nesters. Holes with a larger volume may allow for larger clutch sizes, better thermoregulation by nestlings and/or better protection from predators (Alatalo et al. 1988; Slagsvold 1989; Wiebe and Swift 2001; but see

Wesołowski 2003). Conversely, holes with small entrances may restrict access by medium- and large-sized nest predators (Wesołowski 2002). Among species using non-excavated holes, there may be a trade-off between the potential advantage of larger internal area and the potential disadvantage of larger entrance area. However, among species that use non-excavated holes somewhat regularly (e.g. starlings, bluebirds), clutch size, hatch success and fledge success in non-excavated holes all increased with increasing frequency of use of non-excavated holes (K. Martin, unpublished data). For these species, the potential advantages of non-excavated holes, such as reduced competition for nest-sites and increased hole volume, may outweigh any disadvantages.

Of the five species examined in-depth, starlings selected excavated and non-excavated holes for nesting that were the most similar to each other. Although starlings are considered to be nest-site generalists because they have adapted successfully to nesting in both natural and human-made structures, nest-site selection studies of starlings suggest that they are actually quite specialized in their nest-site preferences (Savard and Falls 1981; van Balen et al. 1982; Wesołowski 1989; Carlson et al. 1998). In an earlier study, we found that starlings preferred nest-sites that were larger internally, closer to grassland edge and in trees with only one hole (Aitken and Martin 2004). These strong nest-site preferences may cause starling populations to be limited by the availability of suitable holes. In an experiment in which we blocked the entrances of preferred nest holes, the number of starling nests declined significantly and did not recover following reopening of the holes (Aitken 2007). Starlings are successful competitors for nest-sites, either through direct interference with other hole-nesters or indirectly through the timing of breeding (Ingold 1994, 1996; Wiebe 2003; Fisher and Wiebe 2006) and, therefore, they may be better able to acquire higher quality non-excavated holes than other less competitive or later nesting species.

We observed an abundant supply of natural (excavated and non-excavated) holes on our predominantly mature sites in British Columbia (12.3 holes/ha), as did Wesołowski (this issue) in the primeval temperate Bialowieza Forest in eastern Poland (16 holes/ha). Excavators were the key hole-making agent providing the majority of natural holes in our mixed coniferous–deciduous forests, while non-excavated holes were more abundant in the mainly deciduous forest in eastern Poland. Interestingly, in both studies, secondary hole-nesters primarily used the more abundant hole type (excavated holes in our study sites, non-excavated holes in Wesołowski's sites). In both studies, it appeared that hole supply exceeded demand, with the majority of holes unoccupied each year (Aitken et al. 2002; Aitken and Martin 2004; Wesołowski, this

issue). Thus, in old forest systems, the role of several critical ecological and environmental factors, such as food supply, predation and environmental conditions, may be just as – or more – important than hole availability in limiting hole-nester densities (Walankiewicz 1991; Wesołowski and Stawarczyk 1991; Newton 1994, 1998; Lohmus and Remm 2005; Remm et al. 2006).

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