Population change and nest tree longevity of a small-island population of Red-breasted Sapsuckers (*Sphyrapicus ruber*) breeding in old-growth temperate rainforest

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ABSTRACT—We recorded the population size and nest tree use of Red-breasted Sapsuckers (*Sphyrapicus ruber*) breeding in coastal, old-growth, temperate rainforest on East Limestone Island, Haida Gwaii, British Columbia, over 31 years (1990–2020). The populations density on the 48 ha island ranged from 10 to 46 occupied nests/km^2, with numbers increasing and then decreasing from 1991 to 2005, followed by a gradual increase between 2006 and 2020. The population size was unaffected by a major windthrow event in 2010 that destroyed about a third of the preferred forest type. Nor did breeding birds avoid the remaining trees left within the blowdown area, suggesting that the retention of isolated dead trees within small forest openings may provide useful breeding sites for sapsuckers. Individual trees were used up to 10 times and continued to be selected for up to 21 years after first use, with use being more prolonged for Sitka spruce (*Picea sitchensis*) than for western hemlock (*Tsuga heterophylla*). Maximum span of use probably exceeds 23 years. There was a significant tendency for trees to be used in consecutive years. Modeling the availability of trees used at least once suggested that in all years there were ample suitable trees available, and hence that the population was not constrained by lack of suitable nest sites. *Received 5 January 2022. Accepted 3 January 2023.*

Key words: cavity-nesting, coastal temperate rainforest, Haida Gwaii, nest tree use, Sitka spruce, western hemlock.

Changement de population et longévité des arbres de nidification chez une petite population insulaire de Pics à Poitrine Rousse (*Sphyrapicus ruber*) se reproduisant dans une forêt pluviale tempérée ancienne

RÉSUMÉ (French)—Nous avons enregistré la taille de la population et l'utilisation des arbres de nidification des Pics à Poitrine Rousse (*Sphyrapicus ruber*) qui nichent dans la forêt pluviale tempérée côtière et ancienne de l'île East Limestone, à Haïda Gwaii, en Colombie-Britannique. La densité des populations sur cette île de 48 ha variait de 10 à 46 nids occupés/km^2, avec une augmentation puis une diminution des effectifs de 1991 à 2005, suivie d'une augmentation progressive entre 2006 et 2020. La taille de la population n'a pas été affectée à la suite d'un chablis majeur qui, en 2010, a détruit environ un tiers du type de forêt préféré par l'espèce. Les oiseaux nicheurs ont continué à utiliser les arbres restants dans la zone de chablis, ce qui suggère que la rétention d'arbres morts isolés dans de petites ouvertures forestières peut fournir des sites de reproduction utiles pour les pics. Certains de ces arbres ont été utilisés jusqu'à 10 reprises et ont continué à être sélectionnés jusqu'à 21 ans après leur première utilisation, l'utilisation étant plus prolongée pour l'épicéa de Sitka (*Picea sitchensis*) que pour la pruche de l'ouest (*Tsuga heterophylla*). La durée maximale d'utilisation dépasse probablement 23 ans. Il y avait une tendance significative chez ces arbres à être utilisés au cours d'années consécutives. La modélisation de la disponibilité des arbres utilisés au moins une fois suggère qu' il y avait chaque année suffisamment d'arbres adéquats disponibles, et donc que la population n'était pas limitée par le manque de sites de nidification appropriés.

Mots clés: épicéa de Sitka,forêt pluviale tempérée côtière, Haida Gwaii, nidification cavicole, pruche de l'ouest, utilisation des arbres de nidification.

Sapsuckers (*Sphyrapicus* spp.) are among the most common woodpeckers in most forested areas of British Columbia, Canada. The genus is represented in the province by 4 largely allopatric species, all similar in size and behavior. Williamson's (*S. thyroideus*) occurs in the southern interior, Red-naped (*S. nuchalis*) in the central interior, Yellow-bellied (*S. varius*) in the boreal northeast, and Red-breasted (*S. ruber*) along the coast and in the central interior (Campbell et al. 1990). Being primary excavators, creating a new nest cavity yearly (Pilgrim et al. 2019, Walters et al. 2020), sapsuckers provide many nest or roost sites for secondary cavity-nesting birds and small mammals (Martin et al. 2004; Cockle et al. 2011, 2019). The breeding biology of these 4 species has been studied in interior (Petersen and Gauthier 1985; Aitken et al. 2002, 2004; Aitken and Martin 2004; Martin et al. 2004) and coastal forests of British Columbia (Joy 2000, Pilgrim et al. 2019).

The Red-breasted Sapsucker breeds in old-growth and mixed-age forests, riparian tracts, fruit orchards, and other non-forest habitats (Campbell et al. 1990, Walters et al. 2020). It is described as an "uncommon resident" in coastal forests and the central interior, with most birds moving from the interior and northern coastal British Columbia in

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winter to southern Vancouver Island and parts of the lower mainland (Campbell et al. 1990).

The extent of old-growth temperate rainforests has greatly diminished in coastal British Columbia due to logging (MacKinnon 2003). Forest management practices relating to the supply of dead and dying trees may have important implications for the suitability of post-harvesting and mature second-growth forests for sapsuckers. There are no conservation concerns specifically for Red-breasted Sapsuckers (Davidson and Seneviratne 2015) and it is considered a secure species (i.e., yellow listed; British Columbia Conservation Data Centre 2019). However, more information is needed on cavity-nesters using dead trees to improve ecosystem-based management approaches, including forest stewardship plans, for overlapping species that are secondary cavity-nesters (Bunnell et al. 2002, Cockle et al. 2011). On Haida Gwaii, these include the listed subspecies of Northern Saw-whet Owl (*Aegolius acadicus brooksi*; Province of British Columbia 2011, British Columbia Conservation Data Centre 2019). Aitken et al. (2002:400) stressed that, to respond to the needs of forest management, better estimates of cavity availability, and more comprehensive data on rates of cavity creation, are needed in British Columbia generally.

Haida Gwaii (formerly the Queen Charlotte Islands) is an archipelago of about 150 forested islands off the north coast of British Columbia. It supports a relatively dense population of Red-breasted Sapsuckers (Davidson and Seneviratne 2015) breeding in old-growth coastal temperate rainforest. We report on a 31-year study of a population breeding on East Limestone Island, Haida Gwaii, within the K'uuna Gwaay Heritage Site and Conservancy, jointly managed by the Council of the Haida Nation and the Province of British Columbia. Based on annual observations of occupied breeding sites, we examined population trends on the island, analyzed how long trees, once used, remained suitable for occupation and how often individual nest trees were reoccupied. We used these results to assess the availability of previously used trees in relation to population density and hence to assess the likelihood that the population is constrained by the availability of nest trees. Although there are several publications dealing with the nest site preferences of the species, none deals with the frequency of repeat use or the longevity of breeding trees over several decades. Our study contributes to an understanding of cavity availability and our results should help to inform forest management practices with respect to the retention of standing dead or dying trees. Information on nest tree and nest site characteristics (e.g., tree height and girth, decay state) for the East Limestone Island population are given by Pilgrim et al. (2019).

Methods

Study area

East Limestone Island (48 ha), on the east coast of Haida Gwaii, is situated off the southeast corner of the much larger Louise Island (27,500 ha) and separated from it by 370 m of open water. It is located in the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1991). Above the wave-splash zone, the island is mostly covered in old-growth coastal temperate rainforest, composed of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). A section of the island along the south coast supports mainly red alder (*Alnus rubra*), much smaller in stature than the conifers, and apparently grown since a fire burned the area in 1950 (Fig. 1, Table 1). All standing trees, whether living or dead, are herein referred to as "trees." The very large canopy trees (>1 m dbh) on East Limestone Island likely do not reach the normal threshold for being considered "old-growth" in coastal forests (250 years old) because of their exposure to winds, but these forests have all the other ecological attributes of coastal old-growth and are thus referred to as old-growth temperate rainforests in this paper. Further details of the study area are given by Pilgrim et al. (2019).

In winter 2010–2011, many mature trees on East Limestone Island were toppled or broken off by wind across the northern portion of the island, with less damage on the east side. Approximately 10 ha of forest (1/3 of the forest used by the sapsuckers) was affected (Fig. 1, inset). For coastal temperate rainforests, windthrow (or blowdown) and landslides are the major sources of ecosystem disturbance and restructuring (Pojar and MacKinnon 2004). We compared the population size and nest distribution of sapsuckers before and after this storm event.

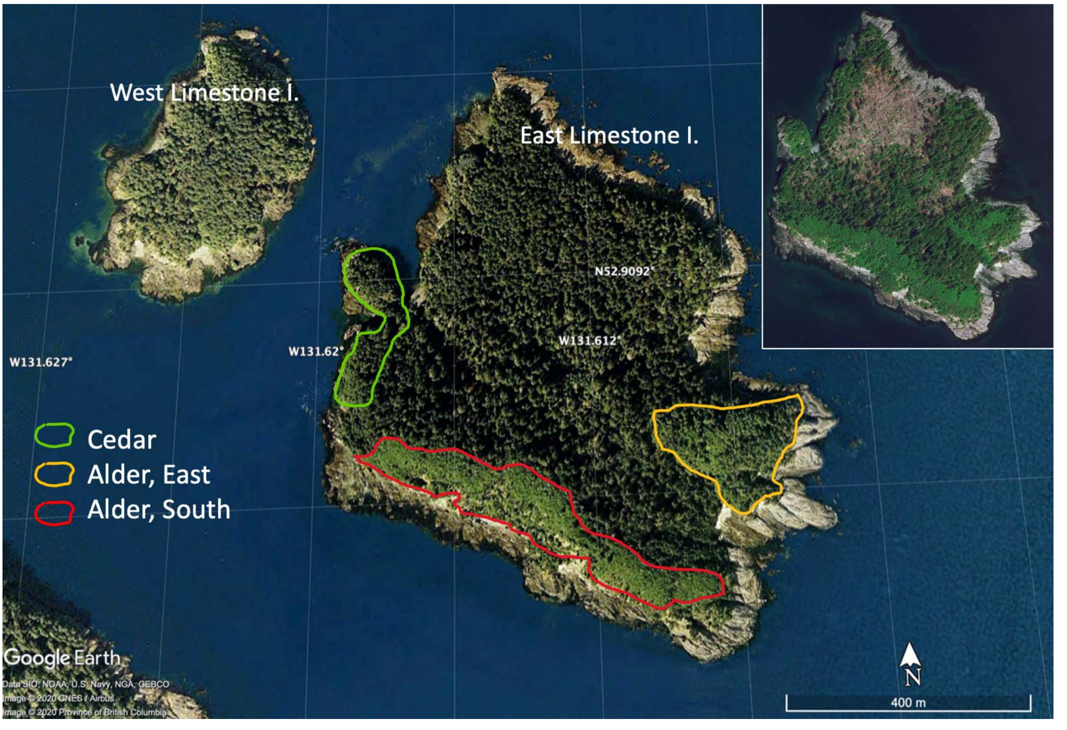

Figure 1. Satellite image of East Limestone Island, Haida Gwaii, British Columbia, showing the forest distribution pre-blowdown: "Cedar" areas comprise pure stands of western redcedar; "Alder South" area comprises predominently red alder; "Alder East" comprises a mixture of red alder, Sitka spruce, and western hemlock; the remainder of the island comprises mixed coniferous forest, predominantly Sitka spruce and westerrn hemlock with infrequent western redcedar. The inset shows the area affected by the 2010–2011 blowdown event (treeless area in the northern half of the island).

Field work

Observations of Red-breasted Sapsucker nest sites were conducted on East Limestone Island from 1990 to 2020. Only 1 site was found in 1990, when observations were incidental to other work, but in all subsequent years systematic surveys to detect occupied breeding sites were carried out annually. A team of 4–6 observers, including trained biologists and citizen science volunteers, was present on the island throughout the Red-breasted Sapsucker breeding season (1 May–30 Jun; median start of incubation 7 May, median fledging 17 Jun; Pilgrim et al. 2019) in every year. More than 200 people were involved in the collection of this data set, from highly experienced ornithologists and students to untrained amateurs. However, the species is very easy to identify, as are the nest holes. With initial training by staff, first-time participants were found to readily recognized both birds and nest cavities. Up to 1995, nests were located by observing birds visiting holes and by listening for begging chicks during the nestling period (Jun). Chick vocalizations are audible up to at least 60 m from the nest tree. A trail system penetrates within 100 m of all parts of the island, allowing dead trees to be easily located over almost all of the area. Out of 344 cavities visited by sapsuckers up to 2018, 219 fledged juveniles (Pilgrim et al. 2019). Hence

Table 1. Area of different forest types on East Limestone Island, Haida Gwaii, British Columbia, as measured from aerial photographs (Fig. 1).

Dominant tree	Area (ha)	Sapsucker trees	Density (nest trees/ha)
Mixed coniferous	32.2	126	3.91
Red alder (Alder South)	8.3	2	0.24
Western redcedar	1.6	0	0
Mixed alder/coniferous (Alder East)	2.9	2	0.69
Total forest	45.0	130	2.89

hearing chicks should allow the location of at least 64% of breeding sites.

From 1996 onward, all trees used over the previous 5 years were observed for periods of 30 min each during 0800–1800 h on a minimum of 3 dates in late April or May (early incubation period). Those where activity was observed in May were revisited for 30 min every 2–3 d during June to determine the presence of begging chicks and the date of fledging. During the June surveys, as well as during other work around the island (usually >10 person-h daily), we watched any sapsuckers seen feeding until they returned to their nest cavities: this enabled some previously undetected sites to be located. Cavities where birds were seen entering more than once were assumed to be used for nesting. We think the combination of watches at nesting trees during incubation, listening for nestling vocalizations, and following feeding birds back to the nest, located most occupied nest sites in every year. This is confirmed by the fact that, after 1995, few sites were located during the nestling period, suggesting that we found most nest sites during incubation. No detailed examination of nest cavities was possible because most nest sites were more than 10 m up (mean 17.3 m; Pilgrim et al. 2019): the rotten state of the trees made climbing inadvisable.

When first located, each nesting tree was marked with a number tag and the position was mapped, originally by reference to local topographic features or known locations on trails, then later using Geographic Positioning System (GPS). Heights of trees and nest holes were measured by geometry (using a clinometer and a measuring tape), and dbh was measured by taking circumference at 1.5 m above ground. Observations at East Limestone Island have shown that Red-breasted Sapsuckers typically excavate their nesting holes in dead trees at Wildlife Tree states 4 or 5, trees without foliage or secondary branches, with decayed heartwood and relatively hard sapwood (Guy and Manning 1995, Pilgrim et al. 2019).

Analyses

To analyze trends in the number of Red-breasted Sapsucker nests found each year, we compared East Limestone Island data with Breeding Bird Surveys (BBS; https://wildlife-species.canada.ca/bird-status [accessed 26 Mar 2020]) for British Columbia Northern Pacific Rainforest region (BCR 5). Data from BBS was available up to 2017 (Smith et al. 2019). Trends were analyzed using linear regression and a breakpoint analysis derived from the Statistica 7.1 piecewise linear regression procedure (Statsoft 2005).

To determine how long trees remained available for nesting, we calculated the duration from the first nest to whenever that tree was found to have blown down. Where trees were damaged or broken off but not uprooted, the remaining tree was considered still available for nesting if it was at least 5 m in height (Pilgrim et al. 2019). To calculate the number of previously used trees available for nesting in a given year, we considered only trees that had been first used in 1996 or later. Trees found in earlier years stand a >50% chance of having been used in years before our study began (see Results). We assumed (1) that trees were suitable for nesting by sapsuckers every year between first and last observed use and (2) that trees that did not fall during the study period were available for at least 5 years from first use (see Results). Given that our estimates of availability are based on these very restrictive assumptions, the true availability in most years was probably much higher and hence our estimates should be treated as lower limits, rather than typical availabilities.

To analyze the span of use (i.e., number of years from first to last observed occupancy), the number of years of active use and the number of years of longest continuous use (consecutive years) of nest trees, we used data from all trees combined, as well as separating western hemlock and Sitka spruce to test for differences between tree species. Because the longest span of use was 21 years, we repeated some analyses only for the sample of trees known to be active during 1990–1998 and hence subject to at least 22 years of observations. Statistical tests and curve-fitting were performed using Statistica 7.1 (Statsoft 2005). Mean values are shown ± 1 SE.

Results

Trends in nest numbers

The mean number of active nests each year from 1991 to 2020 was 12.1 ± 0.8 (range 5–22), giving a mean density for the island of 25 nests/km^2. The mean number of nests per year following the

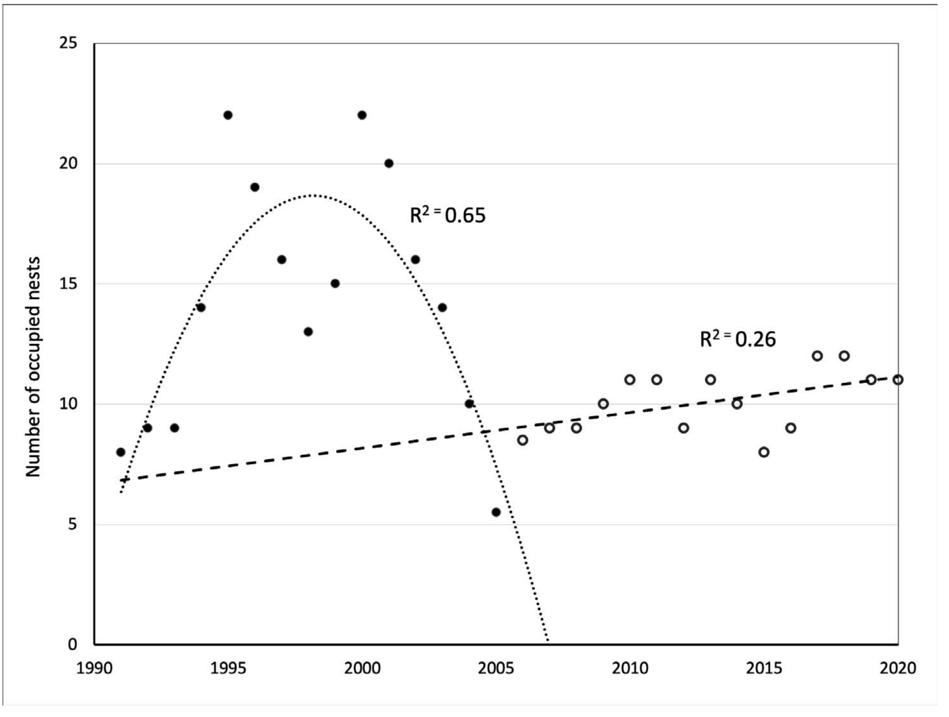

Figure 2. Number of occupied Red-breasted Sapsucker nests found on East Limestone Island, 1991–2020. Fitted regressions are for years before (dotted) and after (dashed) the 2005 breakpoint; breakpoint was determined from a piecewise linear regression procedure.

blowdown of 2010–2011 (mean for 2011–2020 = 10.4 nests) was similar to the mean in the preceding 9 years (mean for 2002–2010 = 9.75 nests).

There was a significant linear decline in nest numbers over the period of the study ($r_{28} = 0.36$, $P < 0.05$; Fig. 2). However, inter-annual fluctuations in numbers of active nests were not random but proceeded in runs of years with positive population change being interspersed with runs of negative changes (Runs test, $Z_{28} = 2.12$, $P < 0.05$). A period of relatively high population during 1994–2003 (lowest year, 14 nests) was followed by a period of lower population during 2004–2020 (highest year, 12 nests). A statistical breakpoint was determined in 2005, with numbers of active nests prior to 2006 having a best fit to a quadratic polynomial regression (Fig. 2; $R^2 = 0.65$) and after 2005 to a linear regression ($R^2 = 0.26$).

Comparison with regional trends

We found no correlation between the number of nests on East Limestone Island and the BBS indices for the whole province (BCR 5; $R^2 < 0.01$). Specifically, the steep and consistent decline in numbers at East Limestone Island between 2000 and 2005 was not represented in the provincial trend (Fig. 3). However, for the period from 2005 to 2017 the steady expansion of the East Limestone Island population (2.8% annually) was similar to that reported for BCR 5 over the same period (2.3% annually, $R^2 = 0.78$).

Density in relation to forest composition

Most nests in identified trees (97%) were in either Sitka spruce or western hemlock; the remainder were in red alder and no hole was excavated in a western redcedar (Table 1). Most nests (96%) were in the mixed coniferous area with the remainder in the alder or mixed alder/conifer forest. The density of sites used over the course of the study was 2.9 nesting trees/ha over the whole area of forest, 3.9/ha in the spruce/hemlock, and 0.3/ha over the rest of the forested area. Annual nest densities varied from a peak of 0.49/ha in 1995 and 2000 to a low of only 0.11/ha in 2005.

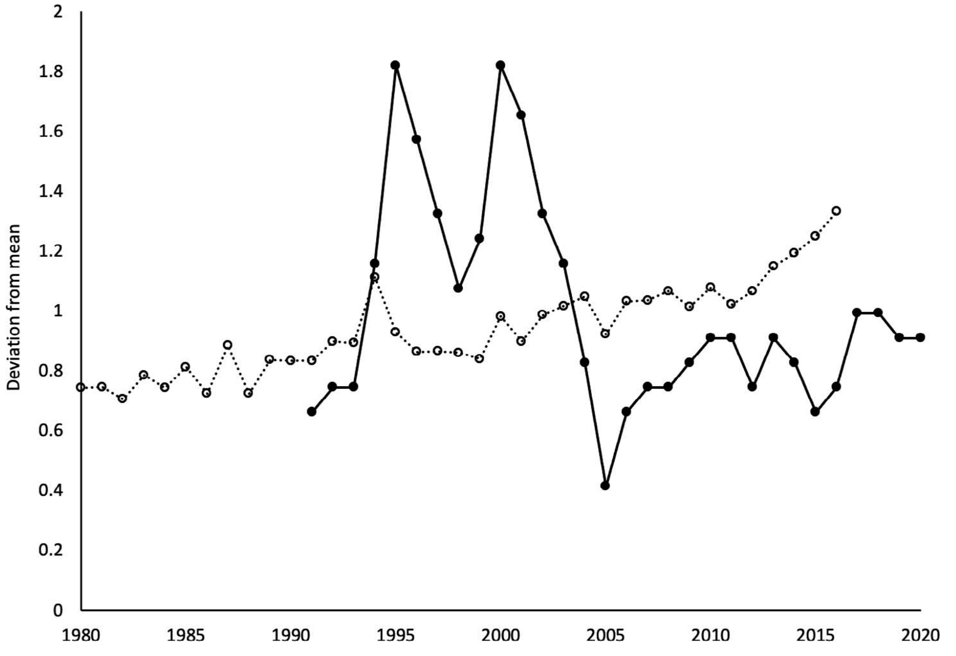

Figure 3. Trends in numbers of Red-breasted Sapsucker nests at East Limestone Island (solid line), compared with trends for Breeding Bird Survey data for British Columbia (dotted line; Smith et al. 2019).

Frequency and duration of use

Individual trees were used up to 10 times during our study, but 46% were used only once; only 10% were used more than 5 times. Only 1 western hemlock was used more than 5 times, but 16% of Sitka spruce were (Fig. 4), with 1 Sitka spruce used continuously for 7 years and another for 9 years. For nest trees located from 1996 to 2015, 42% were used only once and 9% were used more than 5 times. The distribution of the number of times trees were occupied was significantly over-dispersed (aggregated) compared to the Poisson distribution expected if trees were selected randomly each year without reference to previous occupation (Dispersion Test, $\chi^2 = 160$, df $= 99$, $P < 0.001$; based on trees observed 1996–2015).

As previously noted, the maximum time elapsing between first and last use of a nest tree (span of use) was 21 years. When the sample was restricted to trees monitored from 1997 or earlier (tree species combined), then the predicted maximum time to zero probability of use was 23 years, compared with 17 years for the whole sample (Table 2, Fig. 5).

For trees used more than once (54%), the proportion used each year that had been used in the previous year during 1996–2015 did not differ between western hemlock (42%) and Sitka spruce (51%; $\chi^2 = 0.38$, $P > 0.9$). Using our estimate of the proportion of available trees occupied in an average year (44%, see below), it appears that the use of trees in consecutive years is more than twice as likely as the use of other available trees (hemlock, $\chi^2 = 8.9$, $P = 0.003$; spruce $\chi^2 = 32.0$, $P < 0.001$). However, only 6% of trees were used continuously for more than 4 years (Fig. 6).

Availability of potential nest trees

For the sample of nesting trees found in 1997 or earlier, a plot of the proportion still available in relation to span from first occupation gives a close fit to a log distribution (Fig. 5) and suggests that 50% of trees are available for a span of at least 5 years, which we used as our criterion for availability (see Methods). The ratio of the number of trees that were used in each year to our estimates of previously used trees that were available never exceeded 65% (mean 44 ± 2%). The proportion was 65% in 2000, the year of

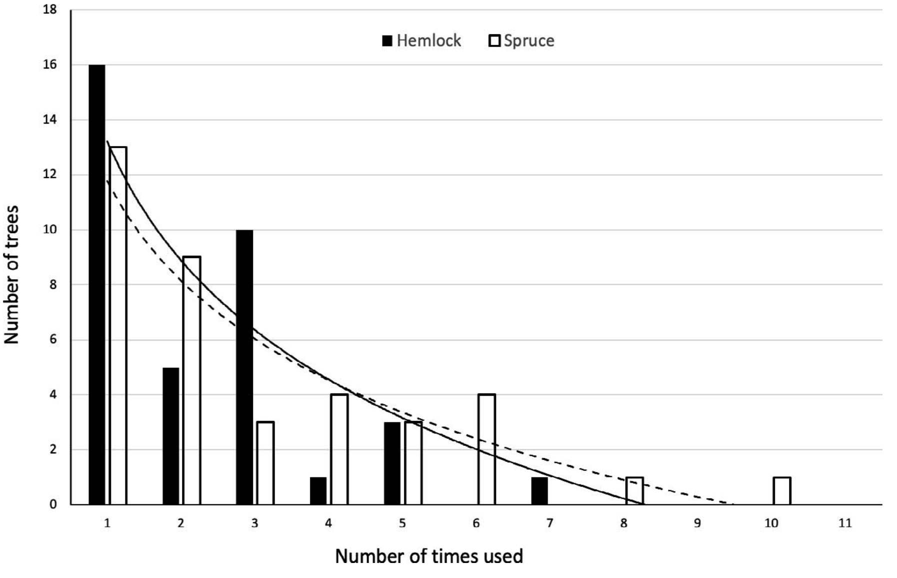

Figure 4. Number of times western hemlock (black bars, solid line) and Sitka spruce (white bars, dashed line) were used on East Limestone Island by Red-breasted Sapsuckers, 1996–2015.

highest breeding numbers, and 52% in 2017 and 2018, the years of highest breeding numbers after the blowdown event of 2010–2011. Given that several trees had spans of use of greater than 15 years, and that some trees marked in the early years of the study were still standing in 2020, our estimates of minimum nest-tree availability were probably very conservative.

Effect of the 2010–2011 blowdown event

Comparing the 10-year periods before and after the blowdown, the ratio of trees used to available trees that had been used previously was higher after the blowdown (mean 47 ± 2%) than before it (40 ± 3%), although the significance level of the difference was low ($t_{18} = 1.74$, $P = 0.20$), but even after the reduction in forest cover, mean minimum availability of nest trees did not exceed 52%. When we compared the proportion of trees used in the blowdown area before and after the event, we found that prior to the blowdown 25% ($n = 15$) of trees used for the first time were within the area of the subsequent blowdown, compared with 42% ($n = 38$) of trees used for the first time after the blowdown (Table 3). Among trees used both before and after the blowdown, 36% ($n = 11$) were

Table 2. Sapsucker nesting trees in East Limestone Island. Comparison of different aspects of the longevity of nesting trees for western hemlock and Sitka spruce (in years, 1996–2015 only; mean ± SE, median, maximum).

	Western hemlock (n = 36)	Sitka spruce (n = 38)	All trees (n = 78)[a]
Number of times used	2.3 ± 0.2, 2, 7	3.0 ± 0.4, 2, 10	2.6 ± 0.2, 2, 10
Longest run of consecutive years used	1.7 ± 0.2, 1, 6	2.1 ± 0.2, 2, 6	1.8 ± 0.1, 1, 6
Span of use (period between first and last nest)	3.8 ± 0.7, 2, 18	4.7 ± 0.8, 3, 15	4.2 ± 0.5, 3, 18[b]
Span of use, 90%	7	12	11
Proportion of nests in trees used in the previous year[c]	60.3% (n = 58)	65.3% (n = 144)	63.9% (n = 202)
Time to destruction for trees that fell during the study	4.4 ± 1.2, 4, 10 (n =14)	8.0 ± 2.5, 8, 14 (n =10)	6.6 ± 0.9, 6, 14 (n =24)

[a] Includes 1 *Alnus*, 3 unidentified conifers.
[b] A tree first used in 1992 was last used after 21 years (falls outside the sample date range).
[c] Includes all nests found after 1991.

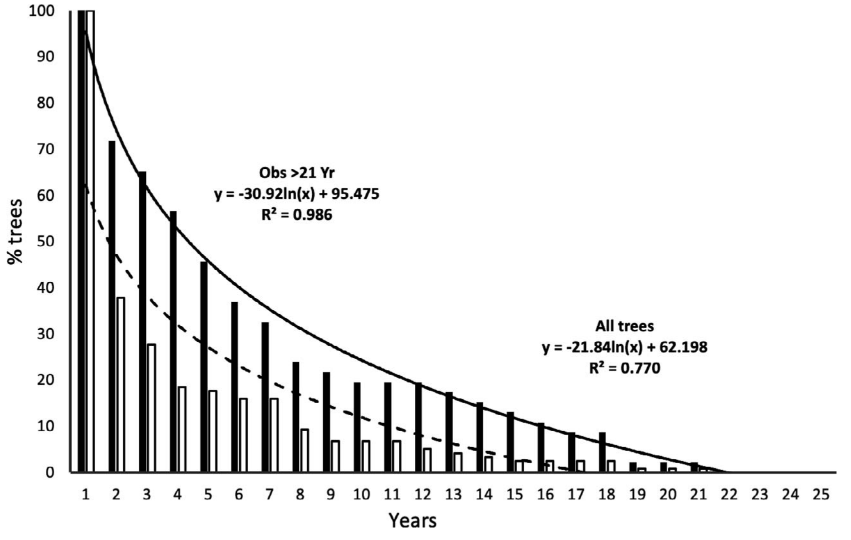

Figure 5. Proportion (%) of trees used by Red-breasted Sapsuckers in East Limestone Island over a given span of years for (1) those first recorded in use before 1998 (black bars, solid line) and (2) all trees for which nesting was recorded (white bars, dotted line).

in the blowdown area. Hence, there is no evidence that the remaining standing trees within the blowdown area were used any less often after the blowdown than trees within the intact forest.

Fallen and broken trees

For the sample of trees where the year of fall was recorded ($n = 22$), the time from the discovery of the first nest to the tree becoming unavailable

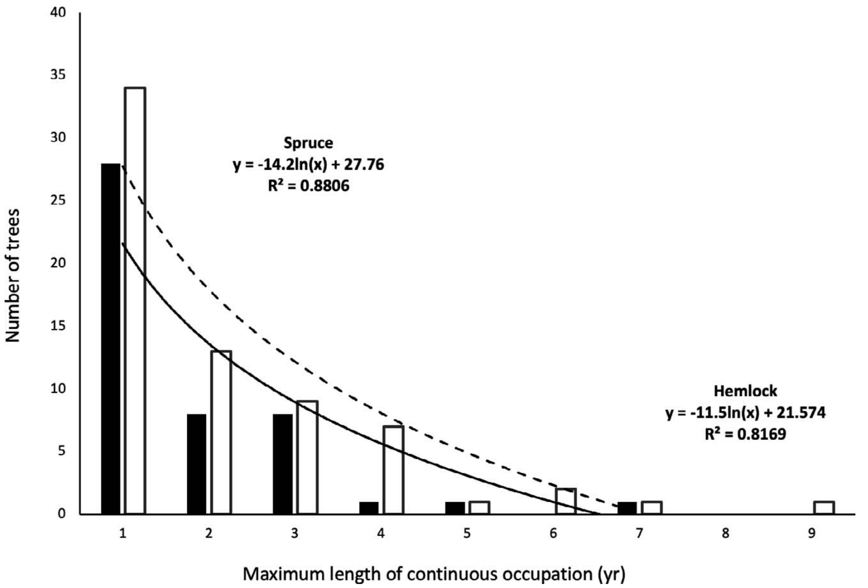

Figure 6. Maximum length of continuous occupation by Red-breasted Sapsuckers for western hemlock (black bars, solid line) and Sitka spruce (white bars, dashed line) trees on East Limestone Island, 1990–2020.

Table 3. Number of trees used by Red-breasted Sapsuckers in East Limestone Island, inside the severe blowdown area (Fig. 1) and in unaffected forest before and after the event (each tree counted only once). Comparing distributions before and after the blowdown, χ^2 (with Yates' correction) = 1.09, $P = 0.30$.

Period	Within blowdown	Unaffected	Totals
2001–2010	5 (25%)	15 (75%)	20
2011–2020	17 (42%)	23 (58%)	40
Used in both periods	6 (36%)	7 (64%)	13

through falling varied from 1 to 14 years (mean 6.2 ± 1.3 years). The duration was significantly longer for Sitka spruce (8.0 ± 1.5 years) than for western hemlock (4.4 ± 1.2 years; $t_{21} = 2.10$, $P = 0.025$). Only 1 tree was occupied in the year before it fell. An additional 19 trees broke off more than 5 m above the ground, creating shorter trees (mean height before truncation = 32.5 m, after truncation = 20.4 m), of which 14 (74%) were used again after the top of the tree had broken off.

Discussion

Given the use of volunteer observers in the study, we need to consider to what extent our results may be influenced by observer effort and experience. The fact that changes in numbers of nests located occurred in runs of years is not consistent with the results being strongly affected by observer error, as such effects would have been random over time. Moreover, most volunteer observers remained in camp for only 1 or 2 weeks so that deficiencies of particular individuals would have been diluted over the nearly 2 month season. The possibility that not all nests were located every year cannot be ruled out, but such omissions would simply increase the degree to which our estimates of wildlife tree availability are likely to be lower bounds (see Methods: Field work). Nor would our comparison of the 2 main tree species, or the effect of the blowdown, be biased by some inter-year variation in the proportion of nests found. Overall, we feel that our analyses are robust to variation in observer skill.

Our results show a relatively high density of breeding Red-breasted Sapsuckers on East Limestone Island compared to observations elsewhere. The mean density of 11 pairs/year (26 pairs/km^2) is similar to that found in riparian forest in western Oregon by Mannan (1977), but higher than several other population densities reported for the species by Walters et al. (2020). Given that numbers reported for the only BBS route on Haida Gwaii (Massett) are the highest for the species anywhere (Walters et al. 2020), and that probability of observation for the species in Haida Gwaii was considered at the top of its range by Davidson and Seneviratne (2015), it seems that Red-breasted Sapsuckers are particularly abundant in Haida Gwaii. It seems that the old-growth coastal temperate rainforest characteristic of the smaller offshore islands of the archipelago provides them with an excellent breeding habitat.

As noted above, Red-breasted Sapsucker nest cavities are frequently used by secondary cavity-nesters. However, in our study area, the main species using sapsucker holes rather than excavating their own were Chestnut-backed Chickadee (*Poecile rufescens*), Tree Swallow (*Tachycineta bicolor*), and Red-breasted Nuthatch (*Sitta canadensis*), all much smaller than the sapsuckers and very unlikely to dispossess them. No evidence for interspecific territoriality with other woodpeckers was observed. Hence, the impact of other cavity-nesting birds on nest-site selection by sapsuckers is not likely to be great.

The annual number of breeding Red-breasted Sapsuckers on East Limestone Island during 1991–2020 trended up and then down until 2005, after which there was a gradual increasing trend. This pattern was not reflected in the national trend in Canada, which was for a 1.7% annual increase during 1970–2016 (1.6% for the "North Pacific Rainforest"; Status of Birds in Canada; https://wildlife-species.canada.ca/bird-status [accessed 17 Apr 2020]). However, after 2005, the increasing trend at East Limestone Island was similar to that observed for the regional population of Red-breasted Sapsuckers. Our results suggest that local, rather than regional, factors influenced the breeding population of East Limestone Island during the period 1991–2005, but that after 2005 the population followed the regional trend for a gradual increase in population. Extensive felling of old-growth forest on Louise Island took place within 5 km of East Limestone Island in the period 1994–2003 (J. Broadhead and D. Leversee, 2019, unpubl. data) but not subsequently. It is possible that such disturbance may have resulted in the relocation of some Red-breasted Sapsuckers, causing immigration to East Limestone Island. The coincidence between logging activity and the peak numbers in our study is suggestive but the hypothesis that the population peak at East Limestone Island resulted from an influx of "logging refugees" remains a speculation.

One of our main aims was to determine the length of time for which dead trees remained usable for sapsuckers. However, although our observations covered 31 years, they may not have revealed the maximum potential span of availability. Many trees used in the first decade of the study were still standing, and in 2019, 1 tree used that year had been occupied, on and off, over a span of 21 years. Moreover, the finding that the modeled occupation span of 17 years for our whole sample increased to 23 years when confined to trees recorded first in 1990–1997, supports the idea that estimates based on shorter runs of years are likely to underestimate the true span over which trees may be available. Despite this potential underestimation and our conservative approach, it appears that ample previously used trees were available for nesting in every year. The fact that the number of nests did not change after approximately one-third of the prime nesting habitat (mixed coniferous) was blown down in the 2010–2011 winter is also consistent with the conclusion that the population is not restrained by lack of breeding sites.

Trees were used in consecutive years more often than we would expect if suitable trees were used at random. We do not know if the same pairs made these consecutive choices, but that seems likely. We did not count the number of woodpecker-drilled holes in each nest tree, but many had several and some >5 holes (authors' unpubl. data). Some may have been drilled and abandoned before we recorded them. It appears that use of the same tree in multiple years is common at East Limestone Island.

Among the 4 common tree species on the island, Sitka spruce and western hemlock were clearly preferred over red alder and western redcedar. Part of the avoidance of red alders may have been related to the age of the alders, many having regenerated following a fire about 50 years prior to the start of our study. All were much smaller than the mature conifers. A random sample of dead trees averaged smaller in height and girth than those actually used by sapsuckers (Pilgrim et al. 2019). Hence the sapsuckers appear to prefer the largest trees. The apparent greater span of usability exhibited by Sitka spruce, when compared with western hemlock, may indicate slower rotting of spruce (Graham and Cromack 1982, Harestad and Keiskerd 1989). This hypothesis is supported by the fact that, among trees that fell during the study, hemlocks exhibited a shorter time between first occupation and the tree falling.

If many trees in the small island rainforests of Haida Gwaii start life as a result of blowdown events, there may be some synchrony in the age of trees over limited areas, even without human intervention. If so, for individual islands, the availability of trees in the preferred decay states 4 and 5 (Pilgrim et al. 2019) may fluctuate over time, depending on the time elapsed since the last major blowdown. The relatively high density of sapsuckers at East Limestone Island during our study may, at least in part, be related to a previous blowdown event that occurred suitably long ago to create a canopy cohort that has now reached senescence. We can predict that, as the blowdown area regenerates and the snags currently in use rot away, that part of the island will provide relatively few opportunities for sapsucker nesting: a situation that could persist for a century or more until the current crop of regenerating trees (mainly spruce) passes maturity.

The species and age of trees used for breeding sites by Red-breasted Sapsucker vary geographically. Among 65 nests reported by Campbell et al. (1990) over the whole of British Columbia, 65% were in deciduous trees, including poplars (*Populus* spp.; 23%), alders (*Alnus* spp.; 19%), and maples (*Acer* spp.; 12%), 13% were in conifers, and the remainder were in unidentified trees, with 67% of nests 3–9 m above the ground. In central interior British Columbia, all 193 nests reported by Martin et al. (2004) were in quaking aspen (*Populus tremuloides*). On the other hand, on Vancouver Island, in high-elevation coastal montane forests, nests were excavated mainly in western white pine (*Pinus monticola*) and Douglas fir (*Pseudotsuga menziesii*; Joy 2000). Similar variation occurs in the state of the trees: all nest trees in high-elevation coastal montane forests on Vancouver Island and in Oregon and northern California were dead (Joy 2000, Walters et al. 2020) whereas most trees in central interior British Columbia (i.e., quaking aspen) were alive. We have shown elsewhere that Red-breasted Sapsuckers in our study area used almost exclusively dead conifers and nested much higher above ground than other nests reported in British Columbia (cf. Campbell et al. 1990, Pilgrim et al. 2019). It needs to be kept in mind that our results for length of use and repeat occupancy of trees at our study site are unlikely to be representative of areas elsewhere, especially those where living broad-leaved trees are preferred.

Perhaps surprisingly, the major windthrow event of 2010–2011, which blew down or broke off most of the trees in a third of the forest, seems to have had little or no impact on the number of Red-breasted Sapsuckers breeding on the island. No tendency to avoid the remaining trees standing in the areas affected by the blowdown could be detected and, in fact, numbers of nests in the blowdown after the event exceeded those in earlier years. This finding suggests that isolated dead trees left in small (ca. 10 ha) forest openings, such as those created by the blowdown, can provide suitable nesting sites for sapsuckers, reducing the impact on the population.

We provide evidence that small, offshore islands containing old-growth spruce-hemlock forests on Haida Gwaii provide an abundance of trees suitable for sapsucker nesting. This abundance is created not just by the periodic decay of mature trees, but by the length of time that they remain potentially available for occupation. Our results suggest that this may be as much as 23 years, although for 90% of spruce the observed period of usability was less than 16 years and for hemlock less than 14 years. These windows of availability may depend on local climate and edaphic factors, influencing the rate of rotting (Basham 1973), as well as on the rate of loss due to windthrow.

Our results demonstrate the value of long-term studies of cavity-nesting birds in determining the potential rate of turnover of nesting trees and hence provide useful information for forest managers on the persistence of wildlife trees. We concur with Cockle et al. (2011:380) who suggested that "governments and forest certification agencies should require forestry companies to conserve a sufficient supply of old trees for wildlife, and to ensure a long-term supply of these trees through careful management of forest age and size structure." In the coastal old-growth forests of British Columbia, this requires both maintenance of individual dead trees for nesting, either individually or in patches of trees within logged areas, and larger intact areas of old-growth forest that will provide suitable dead trees for nesting in the decades to come.

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