

Williamson's Sapsucker (*Sphyrapicus thyroideus*) nest productivity in relation to tree densities in British Columbia.

L. W. Gyug¹, S. Wilson², C. Steeger³, and P. Ohanjanian⁴.

¹Okanagan Wildlife Consulting, 3130 Ensign Way, Westbank, B.C. V4T 1T9 Canada; e-mail: les_gyug@shaw.ca

²EcoLogic Research, 406 Hemlock Avenue, Gabriola Island, B.C. V0R 1X1 Canada; e-mail: steven.wilson@ecologicresearch.ca

³Pandion Ecological Research Ltd., 532 Park Street, Nelson, B.C. V1L 2G9 Canada; e-mail: csteeger@netidea.com

⁴4481 LD Ranch Road, Kimberley, B.C. V1A 3L4 Canada; e-mail: pohanj@xplornet.com

Abstract: We examined the relationship between nest productivity (number of young fledged per nest) and the density of live trees ≥ 18 -cm dbh at 160 Williamson's Sapsucker nests in southern British Columbia from 2006–2008. Mean nest productivity was 3.24 ± 0.11 (SE) and did not vary significantly from year to year or between the three regions where Williamson's Sapsucker breed in B.C. Nest productivity did not vary significantly between open seed tree cuts (< 50 trees/ha) and mature forests (> 150 trees/ha) but 94% of nests in seed tree cuts were within 160 m of forests, well within the observed adult foraging ranges from nests. Nest productivity was significantly lower where average tree densities were < 85 /ha in the breeding territory (225-m radius surrounding a nest). Nest productivity was not affected by tree densities in the nest stand (within 60 m of the nest) but was significantly lower when tree densities were < 85 /ha in the foraging territory (60–225 m from the nest). Habitat targets during timber harvesting within Williamson's Sapsucker breeding territories should retain an average of about 100 trees/ha with this target expected to be met for each breeding territory, but not necessarily at every location within each territory. The target of 100 trees/ha should maintain the average tree density well above the minimum of 85 trees/ha below which nest productivity is reduced.

Key words: Williamson's Sapsucker, *Sphyrapicus thyroideus*, nest productivity, British Columbia

Introduction

Williamson's Sapsucker, *Sphyrapicus thyroideus* (Cassin, 1852), is a medium-sized cavity-nesting woodpecker specialized for feeding on tree sap, and inhabiting the forests of western North America. In Canada, Williamson's Sapsucker is a migratory bird and breeds only in southern British Columbia. It is assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2005), listed on Schedule 1 of the Species-at-Risk Act (July 2006) and requires a recovery strategy that includes the identification of critical habitat.

Williamson's Sapsuckers require trees suitable for excavating nest cavities (Gyug 2009a), for extracting sap (Gyug 2009b), and for gleaning invertebrate prey. Williamson's Sapsucker is specialized for feeding on tree sap but ants are the primary food fed to nestlings (Crockett 1975) and are a major food of the adults (Beal 1911, Otvos and Stark 1985, Stanford and Knowlton 1942). These ants are gleaned primarily from the trunks of live trees (Crockett 1975, Stallcup 1968) as the ants climb the trees to tend aphids. Here we assess

the relationship of Williamson's Sapsucker nest productivity to the density of the foraging substrate, i.e., the live trees from which those prey are gleaned.

There have been few published studies of clutch size, nest productivity or nest success for Williamson's Sapsucker. Clutch size ranges from 3–7 (Bent 1939) but averages between 4 and 5 eggs per nest (Crockett and Hansley 1977, Clark and Martin 2007). Nest productivity averages between 3 and 4 young fledged per nest (Crockett and Hansley 1977, Dobbs *et al.* 1997, McGrath 2004). Nest success has been estimated at 94–97% (Martin and Li 1992, Conway and Martin 1993) using the apparent method (ratio of successful nests to all nests, Johnson 2007) and at 85%–91% calculated from estimates of daily nest survival using a modified Mayfield method (Martin and Li 1992, Clark and Martin 2007). Only one study attempted to correlate any of these life history traits with environmental variables, with no correlations possible because of a lack of variation in nest success with almost all nests being successful (Conway and Martin 1993). Cavity-nesting birds in general have high nest success compared to other birds (Martin and Li 1992), so nest success did not appear to be a good trait to attempt to correlate with

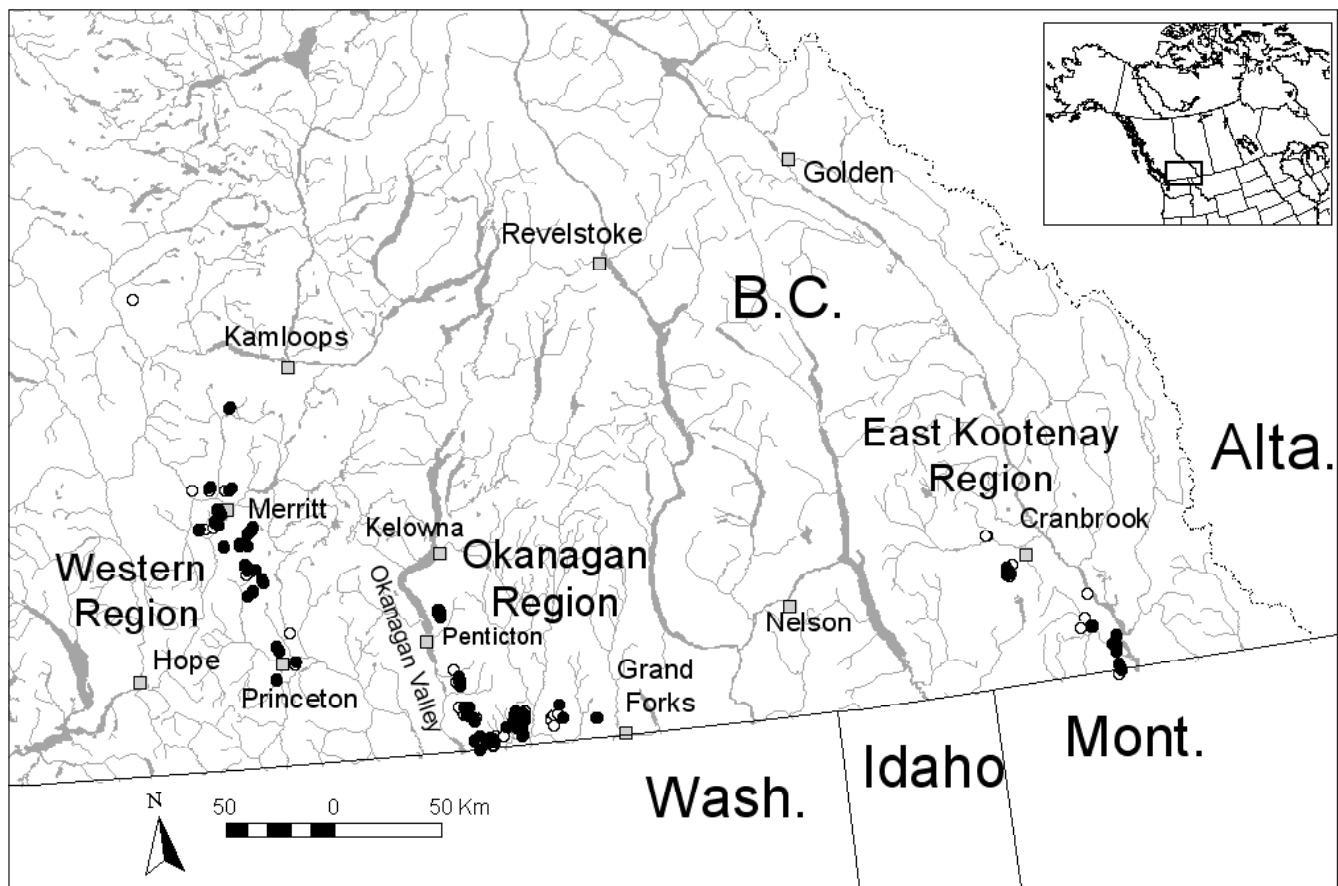


Figure 1. Location of Williamson's Sapsucker nests for which nest productivity was available (black-filled circles) and unavailable (open circles) in the southern interior of British Columbia, 2006–2008.

environmental variables for Williamson's Sapsucker. However, nest productivity did vary depending on whether the male Northern Flicker (*Colaptes auratus*) or both parents were feeding the chicks (Wiebe 2005), so that nest productivity of ant-specialist woodpeckers like Northern Flickers and Williamson's Sapsuckers may be influenced by foraging success.

Prior to 2006, we observed Williamson's Sapsuckers nesting in managed forests of the Okanagan region of B.C. in very open "seed tree" cuts with a few mature trees left as seed sources (5–25 mature trees/ha), stands of intermediate tree density, and in mature forest (>150 mature trees/ha) that was either uncut or regenerated after being partially cut more than 50 years previously. If nests within seed tree cuts are just as productive as nests in mature forests, then critical tree densities in managed forests might be defined very broadly, minimizing potential conflicts between maintenance of productive breeding territories and intensive timber extraction. However, pairs nesting in very open stands seemed to be foraging primarily in nearby dense forests indicating that tree density in the overall foraging area may be as important as tree density immediately adjacent to the nest (Personal observations, L. Gyug, 2004–2005).

The purpose of this study was to assist in defining Spe-

cies-at-Risk critical habitat for Williamson's Sapsucker, and to provide guidelines for forest managers for maintaining productive Williamson's Sapsucker habitat. We postulated that Williamson's Sapsucker nest productivity would be lower in habitats with fewer trees because adults feeding nestlings would have fewer foraging opportunities close to nest trees. We examined this hypothesis post-hoc by analyzing the relationship of nest productivity to tree densities at Williamson's Sapsucker breeding sites, and the effects of distance to mature forests on nest productivity.

Methods

The study area was the interior of southern British Columbia within the breeding range of Williamson's Sapsucker (Figure 1). From 2006–2008, we used call playback surveys to find Williamson's Sapsuckers from late April to early June then searched for nests from mid to late June. We also checked known nest trees from 1996–2005 for breeding activity. Detailed locations, methods and results of the surveys up to 2006 have been described elsewhere (Gyug et al. 2007).

Nest productivity was defined as the number of nestlings raised to 80% of the fledging date, or about 23–24 days of age (Birds and Burns Network 2005a). Approximate age of nestlings was estimated using the developmental rates detailed by Jackson (1977). To count nestlings, a nest pole camera was used for nests <15 m high, and a climber and nest camera were used for nests >15 m. Nest productivity was measured for as many active nests as possible based on budget constraints and safe climbing. The nest camera signal was recorded on a MiniDV video camera through the video input jack so that the number of young in the nest could be verified later. Return visits at 4–7 day intervals were made to nests until the young were estimated to be >22 days old whenever possible. Since our priority was to estimate number of young fledged, and not daily nestling survival rates, often the first nest camera check was delayed until the young were 13–18 days old (based on whether the adults entered the nest to feed the young, or fed them from outside).

To characterize the breeding territory we chose a conservative 16-ha circular plot measured with a 225-m radius because it was half the mean nearest-neighbour nest distance of 450 m (Gyug *et al.* 2007). We assumed that was the average size of a breeding territory in higher quality habitat where a pair could meet all of its foraging requirements. However, breeding territories may be up to 54 ha, or include areas up to 500 m from the nest, based on radio-telemetry of a single breeding male Williamson's Sapsucker in an open seed tree cut in B.C. (Manning and Cooper 1996) and our own personal observations of Williamson's Sapsuckers foraging 400–500 m from nests in open areas. We defined the area within 60 m of the nest as the nest stand, and the remainder of the breeding territory 60–225 m from the nest as the foraging territory.

We sampled tree density of live trees ≥ 18 -cm dbh using

the vegetation protocol for live trees of the Birds and Burns Network (Birds and Burns Network 2005b) with some modifications as described in Gyug *et al.* (2009a, 2009b). We estimated tree density in the nest stand using four 50-m transect plots in cardinal directions around the nest tree, and in the foraging territory using 15 randomly placed 50-m transects. Where the same nest tree was re-used in successive years, or where a different nest tree was used within 60 m of a previously known nest tree, no additional tree density plots were done. Where a different nest tree >60 m but <225 m from a previously used nest tree was active, we estimated tree density in the new nest stand using four 50-m transect plots around the nest tree, and as many new plots as required to have 15 total plots in the foraging territory of the new nest tree.

ANOVA was used to examine the effects of habitat variables on nest productivity. Breeding habitat was known to be different between regions: ponderosa pine (*Pinus ponderosae*) and aspen (*Populus tremuloides*) forest in the west, and western larch (*Larix occidentalis*)—Douglas-fir (*Pseudotsuga menziesii*) forests in the Okanagan and East Kootenay (Gyug *et al.* 2007). In the first analysis we contrasted nest productivity by region and year to determine if data could be grouped, or if nest productivity should be analyzed separately by region or by year. Interaction effects were not considered because nest productivity data were unavailable from the East Kootenay in 2006. In the second analysis we contrasted nest productivity in seed tree cuts (10–50 mature trees per ha) to mature forests (>150 mature trees/ha). In the third analysis we contrasted nest productivity among different levels of tree densities, but for which we did not have any pre-set tree density classes defined. The distance-weighted least squares regression curve of nest productivity vs tree density was examined to determine tree density classes that might be used to differentiate nest pro-

Table 1. Numbers of Williamson's Sapsucker nests and nest productivity (number of young fledged per nest) by region and year in British Columbia, 2006–2008.

Region	Year	Active nests	Nests with camera checks				
			Nests checked	Young fledged per nest	Failed nests	Successful nests	Young fledged per successful nest
		(n)	(n)	(Mean $\pm$ SE)	(n)	(n)	(Mean $\pm$ SE)
East Kootenay	2006	8	0	N/A	-	-	N/A
	2007	10	7	4.29 $\pm$ 0.29	0	7	4.29 $\pm$ 0.29
	2008	14	12	3.00 $\pm$ 0.43	2	10	3.60 $\pm$ 0.16
Okanagan	2006	53	28	2.79 $\pm$ 0.32	5	23	3.39 $\pm$ 0.24
	2007	60	43	3.56 $\pm$ 0.21	3	40	3.83 $\pm$ 0.16
	2008	38	20	3.15 $\pm$ 0.43	5	15	4.20 $\pm$ 0.14
Western Region	2006	16	15	2.87 $\pm$ 0.19	0	15	2.87 $\pm$ 0.19
	2007	26	24	2.92 $\pm$ 1.74	4	20	3.50 $\pm$ 0.28
	2008	28	26	3.62 $\pm$ 0.22	0	26	3.62 $\pm$ 0.22
Total		253	175	3.24 $\pm$ 0.11	19	156	3.63 $\pm$ 0.08

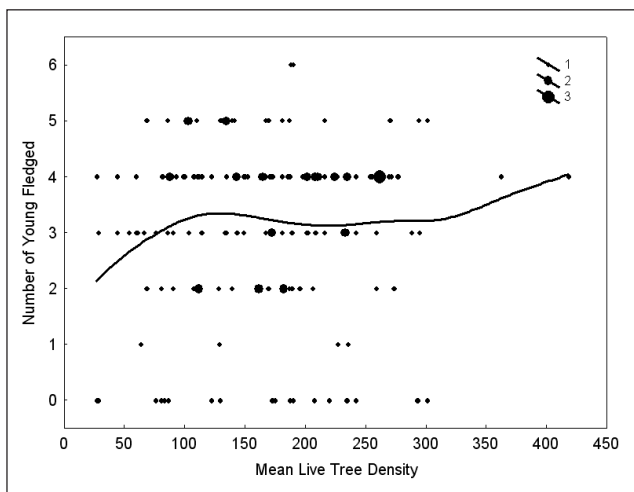


Figure 2. Distance weighted least squares regression curve for number of young fledged against mean tree density (stems/ha) in the breeding territory (16 ha circular area) around Williamson's Sapsucker nests, British Columbia, 2006–2008. Number of nests occupying any given point in the graph is shown by the size of circle.

ductivity using ANOVA. In the fourth analysis, we contrasted nest productivity in the nest stand with the foraging territory for different tree density classes. Finally, to determine if there were any distinct tree density thresholds in occupied breeding territories, the distribution of tree densities in nest stands, foraging territories, and the entire breeding territories were examined for each region. The level for determining significant differences was set at $p = 0.05$.

Results

We determined nest productivity for 43 of 76 nests known to be active in 2006, 74 of 96 nests in 2007, and 57 of 77 nests in 2008. Tree densities were estimated around most nests where productivity was determined (43 in 2006, 73 of 74 nests in 2007, and 44 of 57 nests in 2008). The total of 160 nests for which we had productivity included some nest trees used for several years so that we had full data on 111 unique nest stands.

Nest productivity averaged 3.24 young fledged per nest, and ranged from 0–6 (Table 1). The number of young fledged per nest did not vary significantly by region ($F_{2,155} = 0.466$, $p = 0.63$) or by year ($F_{1,155} = 1.869$, $p = 0.16$).

Nest productivity did not vary significantly ($F_{1,72} = 1.22$, $p = 0.27$) between nests in seed tree cuts (2.81 ± 0.41 , $n = 16$) and in mature forest (3.29 ± 0.20 , $n = 58$). All but one of the nests in seed tree cuts was within 160 m of mature forest, with the final nest 300 m from forest. Three other nests in naturally open nest stands of <50 trees/ha were all within 100 m of mature forests.

The distance weighted least squares regression curve (Figure 2) showed a distinct dip in nest productivity below 85 trees/ha, and a rise above 300 trees/ha. The final rise in the curve from 300–425 trees/ha was based on only 2 nests, i.e., Williamson's Sapsucker only rarely nested in very densely treed stands with >300 trees/ha, so these nests were grouped with the next lower group. Nest productivity was significantly lower ($F_{1,158} = 6.760$, $p = 0.010$) for tree densities of 25–85 trees/ha than for 85–425 trees/ha (Table 2). This was based principally on the much higher percentage of failed nests in the lowest tree density class (25% vs 10%, Table 2) since number of young fledged per successful nest was not significantly different between these classes ($F_{1,139} = 3.254$, $p = 0.07$). Using the same tree density classes, nest productivity was not affected by tree density in the nest stand ($F_{1,157} = 0.15$, $p = 0.70$), but was significantly lower for the lower tree density class in the foraging territory ($F_{1,157} = 5.08$, $p = 0.026$) (Table 3).

Only one nest, and none for which nest productivity was available, occurred where the tree density in the breeding territory was <25 trees/ha, and this appeared to be a critical level below which Williamson's Sapsucker would almost never be found (Figure 3). Very few breeding territories (7.4%, Figure 3) occurred where tree density was <75 /ha. The maximum tree density observed in a breeding territory was an average of 362 trees/ha (Figure 3) even though there were many stands in the regions with tree densities much higher than this (unpublished data).

A significantly higher proportion ($\chi^2 = 11.50$, $p = 0.003$) of East Kootenay breeding territories (43%) were found where there were <100 trees/ha compared to the western region (20%), or the Okanagan (12%). However, tree density in

Table 2. Williamson's Sapsucker nest productivity (young fledged per nest) by tree density class in the breeding territory. Column-wise means followed by like superscripts were not significantly different at $\alpha = 0.05$ determined by one-factor ANOVA.

Tree Density	Active nests	Young fledged per nest	Failed nests	Successful nests	Young fledged per successful nest
	(n)	(Mean $\pm$ SE)	(n)	(n)	(Mean $\pm$ SE)
25-85 trees/ha	20	2.35 ^a $\pm$ 0.36	5	15	3.13 ^a $\pm$ 0.26
85-425 trees/ha	140	3.28 ^b $\pm$ 0.12	14	126	3.64 ^a $\pm$ 0.09
Total	160	3.16 $\pm$ 0.12	19	141	3.59 $\pm$ 0.09

Table 3. Williamson's Sapsucker nest productivity by tree density classes in the nest stand (<60 m from nest) and the foraging territory (60–225 m from nest). Marginal means compared in rows or columns followed by like superscripts were not significantly different at $\alpha = 0.05$ determined by two-factor ANOVA.

Nest stand tree density	Number of young fledged per nest					
	Foraging territory tree density				Total	
	<85 trees/ha		>85 trees/ha			
	(n)	(Mean ± SE)	(n)	(Mean ± SE)	(n)	(Mean ± SE)
<85 trees/ha	7	2.71 ± 0.61	15	3.33 ± 0.39	22	3.14 ^a ± 0.32
>85 trees/ha	15	2.40 ± 0.43	123	3.26 ± 0.13	138	3.17 ^a ± 0.13
Total	22	2.50 ^a ± 0.35	138	3.27 ^b ± 0.13		

breeding territories was not significantly different between regions ($F_{2,132} = 1.99$, $p = 0.14$) with 144.7 ± 16.5 ($n = 28$) trees/ha in the East Kootenay, 178 ± 8.1 ($n = 67$) in the Okanagan, and 169.2 ± 11.8 ($n = 40$) in the western region.

Discussion

Nest trees did not appear to be associated with any particular tree density in their immediate vicinity, i.e. within 60 m. However, density of mature trees over the larger foraging territory was positively correlated with nest productivity. Nest trees were likely selected because of the characteristics that made the individual tree suitable for nesting (Gyug *et al.* 2009a) and because of the average tree density over the wider foraging territory, which was typically >60 m from the nest.

Low tree densities (<85 trees/ha) in the entire foraging territory was negatively associated with nest success driven by a higher number of failed nests rather than through reduced productivity of successful nests. Presumably foraging efficiency was lower in these sparsely treed stands which contributed to nest failure and overall reduced productivity.

For habitat management during timber harvest, cut levels that set the average target higher than the minimum of 85 trees/ha in the entire breeding territory would be prudent, both because post-harvest blowdown or insect kill may reduce this figure, and because this was the minimum level below which nest productivity was reduced. We would suggest that an average of 100 trees/ha be achieved in most breeding territories. Precise densities of leave trees tend to be difficult to achieve operationally because of heterogeneous tree species composition, stand structure and topography, and it would not be expected that this level be achieved throughout the stand, but that this be the average over the entire breeding territory after harvest. This is in the same range of reserve tree densities recommended by Gyug *et al.* (2009a) (i.e., 60–150 trees/ha) that was developed from different principles based on known stand structure in western larch stands containing relatively high densities of very large veteran trees that are most preferred

for nesting. Gyug *et al.* (2009a) also stressed that maintenance of suitable nesting trees within whatever post-harvest targets were set were critical to maintenance of breeding habitat.

Based on general principles only, habitat targets should be set based on existing averages in suitable habitat, rather than to minimum habitat requirements, which may consist of suboptimal habitat at the edge of the normally used range of conditions (Conner 1979). Conner (1979) suggested that levels within one standard deviation of the existing average should be sufficient as a minimum target for species that are not endangered, threatened or sensitive. If applied to Williamson's Sapsucker, then this would be 94 trees/ha (mean of 168, SD of 74). If setting targets at optimum levels (existing averages), then target levels for densities of trees in Williamson's Sapsucker breeding territories should be based on the average tree densities we found (144–175/ha) in the different regions.

While we used nest productivity as a measure of habitat quality, other possible measures are available. Nest success was not considered for this project because, as outlined in the Introduction, it was likely to show too little variation for this species to be an effective correlate with environmental

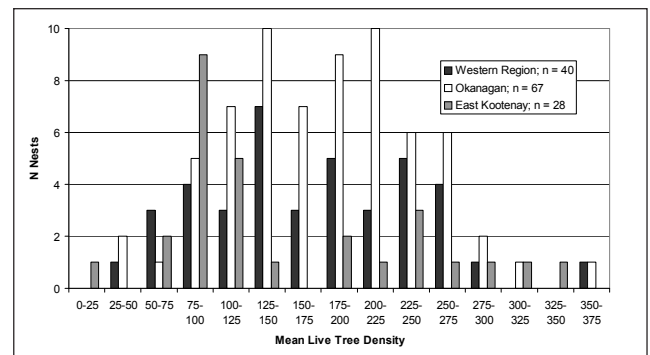


Figure 3. Tree density (stems/ha) of Williamson's Sapsucker breeding territories in British Columbia, 2006–2008. Each breeding territory was only tallied once, even if used for >1 year. Where different nest trees were used within the same breeding territory, the average tree density was used. Breeding territories were included even if nest productivity was not available.

variables. Annual occupancy rates of breeding territories may provide a long-term measure of habitat quality. Breeding density might also be used but only on a scale larger than the individual breeding territory. Breeding density is likely to be a sensitive measure of habitat quality for woodpeckers in general (Drevers *et al.* 2009). However, breeding density should be combined with measures of nest productivity for Williamson's Sapsucker since nest productivity is reduced in sparsely treed stands, and if these make up the majority of nests in an area, then productivity at the landscape level may be low overall.

Acknowledgements

This was a collaborative multi-year project that involved the assistance of many people, some of whom we may have inadvertently missed here, and to whom we apologize in advance if that was the case. For assistance in the field in 2006-2008, the authors would like to thank Jim Beare, A. Michael Bezener, Robin Bentley-Williams, Suzanne Beauchesne, Russell Cannings, Allan Carson, Jerry Clark, Cathy Conroy, John Cooper, Peter W. Davidson, Michael Force, Colin Gyug, Philip Gyug, Shirley Hansen, Felicia Jeulfs, Irene Manley, Maryann McDonough, Christie Megaton, Steve Ogle, Paula Rodriguez de la Vega, Laurie Rockwell, Bruce Ryder, and Nicole Thomas. Major funding for various phases of the project was provided by the B.C. Ministry of Environment, Canadian Wildlife Service, Weyerhaeuser Ltd., Pope and Talbot Ltd, Tembec Industries Ltd., B.C. Timber Sales, the Forest Investment Account of the B.C. Ministry of Forests, and the Council of Forest Industries. Kari Stuart-Smith of Tembec Industries Ltd., Jeff Hoyt, Jared Hobbs and Stewart Guy of the Ministry of Environment, and Kevin Fort of the Canadian Wildlife Service helped initiate portions of this project.

Literature Cited

- Beal, F.E.L. 1911. *Food of the woodpeckers of the United States*. U. S. Department of Agriculture, Biological Survey Bulletin 37. 64 p.
- Bent, A.C. 1939. *Life histories of North American woodpeckers*. U.S. National Museum Special Bulletin 174. 334 p.
- Birds and Burns Network. 2005a. *Changes_needed_in_nest_data_entry.doc*, URL: http://www.rmrs.nau.edu/wildlife/birdsnburns/info_partic.shtml
- Birds and Burns Network. 2005b. *BBN_veg_protocol_with_severity_29_May_2005.doc*, URL: http://www.rmrs.nau.edu/wildlife/birdsnburns/info_partic.shtml [accessed April 2006]
- Clark, M.E. and T.E. Martin. 2007. Modeling tradeoffs in avian life history traits and consequences for population growth. *Ecological Modeling* 209:110-120.
- Conner, R.N. 1979. Minimum standards and forest wildlife management. *Wildlife Society Bulletin* 7:293-296.
- Conway, C.J. and T.E. Martin. 1993. Habitat suitability for Williamson's Sapsuckers in mixed-conifer forests. *Journal of Wildlife Management* 57:322-328.
- COSEWIC. 2005. *COSEWIC assessment and status report on the Williamson's Sapsucker, Sphyrapicus thyroideus, in Canada*. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada. 45 p.
- Crockett, A.B. 1975. *Ecology and behavior of the Williamson's Sapsucker in Colorado*. Ph.D. dissertation, University of Colorado, Boulder, Colorado. 126 p.
- Crockett, A.B. and P.L. Hansley. 1977. Coition, nesting and postfledging behavior of Williamson's Sapsucker in Colorado. *The Living Bird* 16:7-19.
- Doobs, R.C., T.E. Martin and C.J. Conway. 1997. Williamson's Sapsucker (*Sphyrapicus thyroideus*). Number 285 in A. Poole and F. Gill (eds). *The birds of North America*. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C. 20 p.
- Drever, M.L., J.R. Goheen and K. Martin. 2009. Species-energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. *Ecology* 90:1095-1105.
- Gyug, L.W., I.Ohanjanian, C. Steeger, I.A. Manley and P.W. Davidson. 2007. Distribution and density of Williamson's Sapsucker (*Sphyrapicus thyroideus*) in British Columbia, Canada. *British Columbia Birds* 16:2-15.
- Gyug, L.W., C. Steeger and I.Ohanjanian. 2009a. Characteristics and density of Williamson's Sapsucker nest trees in British Columbia. *Canadian Journal of Forest Research* 39:2319-2331.
- Gyug, L.W., C. Steeger and I.Ohanjanian. 2009b. Williamson's Sapsucker (*Sphyrapicus thyroideus*) sap trees in British Columbia. *British Columbia Birds* 19:6-12.
- Jackson, J.A. 1977. How to determine the status of a woodpecker nest. *Living Bird* 15:205-221.
- Johnson, D.H. 2007. Estimating nest success: a guide to the methods. *Studies in Avian Biology* 34:65-72.
- Manning, E.T. and J.M. Cooper. 1996. Progress Report (Year 1 – 1996). *An assessment of woodpecker foraging, home range and patch utilization at Wallace Creek, British Columbia*. Unpublished report prepared for Ministry of Environment, Penticton, B.C. 9 p.
- Martin, T.E. and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579-592
- McGrath, L.J. 2004. Part 1 of annual progress report, birds and burns network, San Juan National Forest. Fire effects on populations and habitats of sensitive species of wildlife in ponderosa pine forests in the Piedra River Basin, San Juan National Forest Colorado (SJCO) Pre

- Burn Investigations. 12 p. <http://www.rmrs.nau.edu/lab/4251/birdsnburns/> [Accessed July 2005]
- Otvos, I.S. and R.W. Stark. 1985. Arthropod food of some forest-inhabiting birds. *Canadian Entomologist* 117: 971-990.
- Stallcup, P.L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. *Ecology* 49:831-843.
- Stanford, J.S. and G.F. Knowlton. 1942. Food of some Utah birds. *Auk* 59: 580-581.
- Wiebe, K.L. 2005. Asymmetric costs favour female desertion in the facultatively polyandrous Northern Flicker (*Colaptes auratus*): a removal experiment. *Behavioral Ecology and Sociobiology* 57:429-437.



Tim Zurovski