

The effects of selective logging on nest-site selection and productivity of hooded warblers (*Wilsonia citrina*) in Canada

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Abstract: We examined nest-site selection by hooded warblers (*Wilsonia citrina*) in two forests differing in composition (extensive pine plantation versus largely deciduous) and management (recent selective logging versus minimal logging). We measured habitat at 52 nests and 66 controls in one forest and 57 nests and 41 controls in the second. Nests had denser ground vegetation, fewer tree stems, less basal area due to small trees and greater basal area due to large trees than controls in both forests. In the managed forest with extensive pine plantations, hooded warblers were in coniferous and logged stands more often than expected by chance, nests had more stumps and greater canopy height than controls, and 91% (52/57) of all nests were found in gaps, 84% of which were created by harvest. Gap age was 6.2 ± 0.9 years (mean \pm SE) in 1999, and 7.6 ± 0.6 years in 2000. In the managed forest, 52% of 24 nests were parasitized in 1999 and 39% of 33 nests were parasitized in 2000. The daily survival rate was 0.936 ± 0.019 in 1999 and 0.944 ± 0.014 in 2000. Successful nests did not differ from unsuccessful nests in any habitat variable. To benefit hooded warblers, forest managers should mimic natural gap creation by using selective logging to create gaps no larger than 0.05 ha, and should leave a residual basal area of mature trees (>38 cm diameter at breast height) of at least 12 m²/ha.

Résumé : Nous avons examiné comment se fait le choix du site de nidification chez la paruline à capuchon (*Wilsonia citrina*) dans deux forêts distinctes par leur composition (grande pinède contre forêt dominée par les feuillus) et par leur gestion (coupe sélective récente contre coupe minimale). Nous avons mesuré l'habitat près de 52 nids et à 66 sites témoins dans l'une et près de 57 nids et à 41 sites témoins dans l'autre. Près des nids, dans les deux forêts, la végétation au sol était plus dense, il y avait moins de troncs, la surface terrière occupée par de petits arbres était plus restreinte et celle couverte par de grands arbres, plus importante qu'aux sites témoins. Dans la forêt aménagée où les pins dominaient, les parulines se tenaient plus souvent dans les zones de conifères et dans les zones coupées que ne le voudrait le hasard; de plus, les habitats autour des nids comptaient plus de souches, le couvert végétal y était plus haut qu'aux sites témoins et 91 % des nids (52/57) étaient construits dans des trouées dont 84 % étaient dues à la coupe. L'âge moyen des trouées était de $6,2 \pm 0,9$ ans en 1999 et de $7,6 \pm 0,6$ ans en 2000. Dans la forêt aménagée, 52 % des 24 nids en 1999 et 39 % des 33 nids étaient parasités. Le taux de survie quotidien a été estimé à $0,936 \pm 0,019$ en 1999 et à $0,944 \pm 0,014$ en 2000. Les nids réussis et les nids ratés ne différaient par aucune des variables de l'habitat. Pour avantager les parulines à capuchon, les gestionnaires des forêts devront reproduire les trouées naturelles et procéder à une coupe sélective pour créer des trouées d'au plus 0,05 ha et conserver une surface terrière couverte d'arbres à maturité (de plus de 38 cm de diamètre à hauteur de poitrine) d'au moins 12 m²/ha.

[Traduit par la Rédaction]

Introduction

Forest loss, fragmentation, and degradation have adversely affected many Neotropical migratory bird species in eastern North America (Robinson and Wilcove 1994; Faaborg et al. 1995). The response of bird species to fragmentation has been well documented, with area-sensitive species disappearing

from many small fragments, and those that remain generally suffering from increased levels of predation and cowbird parasitism and decreased pairing success (reviewed by Donovan et al. 1995). Selective logging, which changes the quality of the forest but does not reduce its area, produces mixed results for forest bird species.

Multiple gaps in a forest caused by single-tree-selection or group-selection logging have the potential to affect bird populations by introducing edge into otherwise continuous forest (Thompson et al. 1993; Robinson and Robinson 1999). Indeed, the abundance of red-eyed vireos (*Vireo olivaceus*) and ovenbirds (*Seiurus aurocapillus*) has been found to be lower in selectively cut stands than uncut stands in southern Illinois (Robinson and Robinson 1999), and the reproductive success of ovenbirds has been found to be lower in selectively cut than in uncut stands in New Brunswick (Bourque and Villard 2001). However, selective logging appears to have a neutral or positive effect on many other bird species (Whitcomb

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et al. 1977; Germaine and Vessey 1997; Robinson and Robinson 1999). Carolina wrens (*Thryothorus ludovicianus*), white-eyed vireos (*Vireo griseus*), hooded warblers (*Wilsonia citrina*), eastern towhees (*Pipilo erythrophthalmus*), indigo buntings (*Passerina cyanea*), and northern parulas (*Parula americana*) have all been found to increase in abundance for a distinct yet limited period after gap creation (Annand and Thompson 1997; Robinson and Robinson 1999), and from a study of forest bird nesting success in single-tree-selection stands in Arkansas it was concluded that this type of management did not appear to affect nesting success (Barber et al. 2001). Forest gaps created as a result of selective logging provide important foraging habitat during breeding (Fuller 2000) and on migration (Blake and Hoppes 1986; Kilgo et al. 1999) because of higher resource abundance in gaps than in closed-canopy forest (Blake and Hoppes 1986).

We studied nest-site selection by hooded warblers in two forest tracts in Canada at the northern edge of the species' breeding range. The hooded warbler is a small forest-interior Neotropical migrant found throughout the northeastern United States and extreme southern Canada that has been reported to nest mainly in shrubby gaps in mature, primarily deciduous forests (Evans Ogden and Stutchbury 1994; Kilgo et al. 1996). Rates of detection of hooded warblers during point counts have been shown to increase after group-selection and single-tree-selection logging, presumably because of the surge in understory plant production in the resulting gaps (Whitcomb et al. 1977; Annand and Thompson 1997; Robinson and Robinson 1999).

Hooded warblers are listed as "threatened" in Canada because the small population (144–207 pairs; McCracken et al. 1998³) breeds almost solely in the Carolinian Forest Zone in southwestern Ontario (Gartshore 1988), where forest loss over the last century has reduced overall forest cover to less than 30% in most counties (Riley and Mohr 1994). Despite this, the Ontario hooded warbler population appears to be stable or even increasing in areas of suitable habitat (M.E.G., unpublished data). We studied hooded warblers in two of the largest remaining forest tracts in southwestern Ontario, which differ considerably in tree species composition and management history. One site, which has extensive pine plantations, has been thinned and selectively logged (group and single-tree selection) over the last 15 years, whereas the second site, which is primarily deciduous and located 6 km away, has had much less logging since 1986. Over the last 5 years, hooded warblers have been increasing in the coniferous site and decreasing in the deciduous site (J.D.M. and M.E.G., unpublished data). Together, these two forests support up to 40% of the known Canadian breeding population of hooded warblers.

Since the largest concentration of hooded warblers in Canada currently nest in a forest consisting of extensive pine plantations, and only one previous study has examined nest-site selection by hooded warblers in this habitat type (Hazler 1999), it is important to characterize nest sites and determine whether birds are nesting successfully in this habitat. Furthermore, no study has examined the characteristics (e.g., size, age, origin) of gaps used by hooded warblers, or examined

the relationship between territory presence and selective logging for this species in Canada, information that could be used in the development of forest-management guidelines (a goal of the National Recovery Plan for hooded warblers; Friesen et al. 2000). Finally, in a recent paper (Bisson and Stutchbury 2000) examining habitat selection by hooded warblers in various forest tracts (including part of one of our study sites) in southwestern Ontario it was suggested that forest maturity is not a limiting factor in nest-site selection by this species, and we wanted to reexamine this conclusion.

The objectives of our study were to (i) characterize nest sites of hooded warblers in relation to forest type, gap characteristics, and recent logging history; (ii) measure the productivity of the largest Canadian population of hooded warblers; and (iii) link productivity to habitat characteristics. We discuss our results in terms of forest-management guidelines that could benefit hooded warblers and other gap-dependent species in the fragmented forests of southwestern Ontario.

Materials and methods

Study area

This study was conducted in the nursery tract of the St. Williams Crown Forest (1213 ha; 42°42'N, 80°28'W) and 6 km west in the South Walsingham Forest (730 ha); both are located in Norfolk County, Ontario, Canada. We refer to the two sites as St. Williams and South Walsingham.

Both sites are dominated by well-drained Plainfield soils and consist mainly of dry sand ridges intergrading with low, wet plains (Gartshore et al. 1987). South Walsingham is dominated by mature, natural deciduous stands, though there are also a few small (2–10 ha) conifer plantations. St. Williams has extensive pine plantations that are approximately 80 years old (Wynia 1990) and up to 50 ha in size. Forest stands in South Walsingham are approximately 75% deciduous, 3% coniferous, and 22% mixed forest, while stands in St. Williams are approximately 26% deciduous, 29% coniferous, and 45% mixed forest, although 65% of the mixed forest is predominantly (>50%) coniferous.

At both sites, conifers include white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and, in St. Williams, several planted stands of Scots and jack pine (*Pinus sylvestris* and *Pinus banksiana*). In St. Williams, red pine are managed for utility poles and white pine are managed for saw logs (Wynia 1990). Most logging occurs in the form of group or single-tree selection, or thinning of the pine plantations. Some harvest of deciduous trees has occurred at both sites. Approximately 50% of St. Williams has experienced some form of cutting since 1986, whereas only about 12% of South Walsingham has been logged. Both forests have a trail system created for forest management, but St. Williams has many additional trails created and used by all-terrain vehicles and dirt bikes. South Walsingham also has some trails used by all-terrain vehicles, but the system is less extensive than that found in St. Williams.

Deciduous trees, which dominate most of South Walsingham and parts of St. Williams, include red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), large-toothed aspen

³J.D. McCracken, D. Martin, I. Bisson, M. Gartshore, and R. Knapton. 1998. 1998 surveys of Acadian flycatchers and hooded warblers in Ontario. Unpublished report by Bird Studies Canada to the Canadian Wildlife Service and Environment Canada Action 21 program, Port Rowan, Ont.

(*Populus grandidentata*), trembling aspen (*Populus tremuloides*), black cherry (*Prunus serotina*), basswood (*Tilia americana*), white oak (*Quercus alba*), black oak (*Quercus velutina*), white ash (*Fraxinus americana*), silver maple (*Acer saccharinum*), sugar maple (*Acer saccharum*), and red maple (*Acer rubrum*). Common understory shrubs at both sites include blackberry (*Rubus* spp.), witch hazel (*Hamamelis virginiana*), American hazel (*Corylus americana*), red maple, red-berried elder (*Sambucus pubens*), eastern flowering dogwood (*Cornus florida*), cherry (*Prunus* spp.), poison ivy (*Toxicodendron radicans* s.l.), spice bush (*Lindera benzoin*), maple-leaved viburnum (*Viburnum acerifolium*), grape (*Vitis* spp.), wood fern (*Dryopteris* spp.), bracken fern (*Pteridium aquilinum*), dwarf chinquapin oak (*Quercus prinoides*), and hawthorn (*Crataegus* spp.).

Nest-site characteristics

From late May to late July in 1995–1997 (South Walsingham) and 1999–2000 (St. Williams) we located hooded warbler territories. We defined a territory as an area in which a male was heard singing on at least two occasions separated by at least 1 week. We traversed all parts of both forests several times, following the extensive trail systems (which allowed accurate mapping of each male and nest), to ensure the detection of all possible territories. We flagged territories, georeferenced them with a GPS, and searched them carefully for nests.

Immediately following each year's breeding season, we measured habitat characteristics around nest and control sites. Because South Walsingham data were originally collected as part of a different study (McCracken et al. 1998⁴), control sites were chosen in a different manner than in St. Williams. In South Walsingham we measured habitat characteristics at control sites at 100-m intervals along a series of transects spaced 200 m apart. In St. Williams, we selected control sites from among the intersections of a 250 × 250 m grid overlaid on a map of the forest; points less than 100 m from any hooded warbler nest, territory site, or forest edge were excluded. A subsample of the resultant points was selected to approximately match the proportions of the overall habitat types used by hooded warblers (see Results). If a sampling site landed on a trail, we walked 20 paces into the forest in a randomly chosen direction.

In both South Walsingham and St. Williams, we measured the following characteristics within a 11.28 m radius (0.04 ha; James and Shugart 1970) of each nest and control site: (i) Size class and species of each living tree and size class of standing dead trees (>2 m in height) and tip-up logs: we used a metre stick marked with tree size classes (Biltmore Reach Stick; James and Shugart 1970) to place each living tree, as well as each standing dead tree and tip-up log, >2 m tall and 3 cm diameter at breast height (DBH) in one of the following DBH size classes: S (sapling), 3–8 cm; A, 8–15 cm; B, 15–23 cm; C, 23–38 cm; D, 38–53 cm; E, 53–69 cm; F, 69–84 cm; G, 84–102 cm; H, >102 cm (James and Shugart 1970). We estimated total basal area (m²/ha) using the following equation (from James and Shugart 1970):

$$\begin{aligned} \text{total basal area} = & [S(0.002) + A(0.0093) + B(0.0279) \\ & + C(0.0744) + D(0.1674) + E(0.2883) \\ & + F(0.4557) + G(0.6603) + H(0.744)]/0.04 \end{aligned}$$

We also calculated basal area separately for the small trees category (DBH 3–38 cm) and the large trees category (DBH >38 cm). (ii) Canopy cover: we used an ocular tube consisting of two pieces of pipe with a diameter of 1.5 cm connected at a 45° angle with a mirror inside and cross-hairs at one end, to allow a person standing upright and looking forward to see the overhead canopy. If leaves were visible in the cross-hairs of the ocular tube, we recorded a score of 1. If no leaves were visible in the cross-hairs, we recorded a score of 0. This measurement was made above 10 evenly spaced locations along each of two transect lines that bisected the sample circle into quarters. Observations were then tallied and multiplied by 5 to provide an estimate of percent canopy cover. (iii) Vegetation density at four levels above the ground: we used a density board consisting of a sheet of cloth 3 m tall by 0.3 m wide marked with 150 alternating blue and white 10 × 6 cm boxes to measure the amount of vegetation obscuring the boxes at four strata above the ground: 0–0.3 m (15 boxes), 0.3–1 m (35 boxes), 1–2 m (50 boxes), and 2–3 m (50 boxes) (Robbins et al. 1989). We held the board 11.28 m from the centre of each sampling site in each of the four cardinal directions and counted the boxes that were more than 50% obscured by leafy plant matter. We averaged the percentages of boxes obscured in each stratum over the four directions. (iv) Dominant shrub genera: we noted the principal species that were present in the shrub layer within each plot.

We measured the following additional characteristics around nest and control sites in St. Williams only: average canopy height (based on the height of four representative trees, measured with a clinometer, within the 11.28 m radius circle), distance to the nearest trail, number of cut stumps, basal area of cut stumps, and dimensions, age, and origin of gaps. Gaps were defined as distinct holes in the forest canopy that had a minimum diameter of 5 m (Brokaw 1982). To determine gap size, we estimated by eye the length of a pair of perpendicular lines in the gap, such that the first (*L*) was the longest straight line that would fit in the gap and the second (*W*) was the longest straight line that would fit in the gap, with the constraint that it was perpendicular to the first (Runkle 1992). The area of the gap was estimated using the equation for the area of an ellipse: $A = \pi LW/4$. Gap origin was determined as harvest, windfall, or dead tree. When a gap was created by harvest, its age was estimated from logging records (when available). When a gap was created by dead or fallen tree(s), its age was estimated from the release date of white pine saplings (Runkle 1992) or the growth rings of small shrubs, assuming that their life-span equalled the time since the gap was created. When using the latter method, rather than logging records, the 1999 field team tended to overestimate gap age by 3.7 years, on average, based on a sample of 13 gaps, and the 2000 field team tended to underestimate gap age by 2.8 years, on average, based on a sam-

⁴J.D. McCracken, D. Lepage, C.M. Francis, and A. Couturier. 1998. Management of the South Walsingham forest complex for forest-interior birds. Unpublished report by Bird Studies Canada to the Ontario Ministry of Natural Resources, Long Point Region Conservation Authority, Norfolk Land Stewardship Council and Norfolk Field Naturalists, Port Rowan, Ont.

ple of 16 gaps. We corrected for this observer difference in each year by subtracting 3.7 years from gaps aged using the release-date method in 1999 ($n = 3$) and adding 2.8 years to gaps aged using the release-date method in 2000 ($n = 5$).

Stand type and logging history

In St. Williams we classified each stand as coniferous ($\geq 80\%$ coniferous trees), deciduous ($\geq 80\%$ deciduous trees), or mixed (21–79% coniferous trees), using the Ontario Ministry of Natural Resources (OMNR) Forest Resource Inventory (FRI). We also used OMNR logging records (primarily forest-resource licences, tenders, and area foresters' reports) to determine the volume (m^3/ha) of trees removed between 1986 and 2000 in each stand. The last logging event in St. Williams prior to this study occurred in March 1997. Most records indicated the number (N), volume (V), and average diameter (D) of trees removed. In cases where volume was not noted (3 forest stands), we estimated V using available data. Precise volume calculations require data on tree species and height (Honer 1967); because we did not have these data we estimated V using the equation $V = NDK$, where K is a constant representing the relationship between V , D , and N , estimated by regression from stands for which all three variables were available ($n = 25$). We categorized each stand according to logging intensity: none, low (0–50 m^3/ha removed), moderate (51–100 m^3/ha removed), and high (>100 m^3/ha removed).

We then overlaid hooded warbler territory locations (based on either nest location or, when a nest was not found, the most common perch of a singing male) in 1999 and 2000 on maps of timber stands indicating stand type and logging intensity. We calculated the expected number of territories in each stand type based on the total area of each stand type available in the forest, assuming an even distribution of territories among stand types. We then compared observed and expected values to determine whether hooded warblers were more likely to be found in stands of particular composition or logging history.

Productivity

We determined the productivity of hooded warblers in St. Williams in 1999 and 2000 by monitoring nests every 3–5 days. We noted the clutch size (number of hooded warbler eggs), whether the nest had been parasitized by cowbirds and the number of cowbird eggs, and the number of hooded warbler chicks that hatched and the number that survived to 5 days. Hooded warblers normally fledge at 8 days of age (Evans Ogden and Stutchbury 1994), but 5 days was the age at which chicks in our study area were banded and nests were last visited, so we calculated survival to this age.

Statistical analyses

To examine nest-site selection, we pooled nests from 3 years in South Walsingham because samples were small (16 nests in 1995, 18 in 1996, and 18 in 1997). We examined nests in St. Williams separately for 1999 and 2000 because samples were larger (24 and 33 nests, respectively). We emphasize the 1999 data from St. Williams because habitat data for both nest and control sites were collected that year. Data from St. Williams in 2000 were used to determine whether patterns detected in 1999 still held in 2000. We initially used

a likelihood-ratio test to compare logistic regression models with all habitat variables (see Table 1 for a list of variables) against a model without habitat variables for each site. Given that these were highly significant, we then made univariate comparisons between hooded warbler nests and controls within each forest using Wilcoxon's rank-sum tests to determine which variables differed between sites. We did not make Bonferroni corrections for these analyses because we had already shown that there were significant overall effects, and we wanted to minimize the risk of overlooking important differences for individual variables. We then used stepwise logistic regression, using only those variables that were collected in both St. Williams and South Walsingham, to determine which variables best discriminated nest sites from control sites in both forests. The classification accuracy of each model was judged with a jackknife concordance estimate.

We used a χ^2 test to compare the numbers of nest and control sites associated with gaps, and to compare the observed and expected frequencies of hooded warbler territories in St. Williams in stands that differed in composition and logging intensity.

To calculate productivity we estimated daily survival rates based on Mayfield's (1975) method over the incubation and chick-rearing stages, with standard errors calculated following Hensler and Nichols (1981). We calculated daily mortality rates across the nesting cycle as the total number of failures divided by the total number of observation days pooled across all nests. The daily survival rate was calculated as $(1 - \text{daily mortality rate})$. Nest success was based on the estimated daily survival rate raised to the exponent that reflects the average length of the nest period under study (Mayfield 1975). We calculated nest success from the first day of incubation to the date when chicks reached 5 days of age (17 days total). Nests that were found after the young reached 5 days were not included in the calculations of daily survival rate or nest success. We compared all nest-site characteristics between successful nests (at least one hooded warbler young raised to 5 days of age) and unsuccessful nests (no young, or only cowbird young, raised to 5 days of age) in St. Williams in 1999 and 2000, using Wilcoxon's rank-sum tests.

All values are presented as means \pm SE or, for highly skewed variables, medians and interquartile ranges.

Results

Nest-site characteristics

We measured habitat characteristics surrounding 52 nests (16 in 1995, 18 in 1996, and 18 in 1997) and 66 controls (all in 1996) in South Walsingham and 57 nests (24 in 1999 and 33 in 2000) and 41 controls (all in 1999) in St. Williams. Habitat around nests differed from that at control sites in South Walsingham ($\chi^2 = 49$, $df = 15$, $P < 0.0001$) and St. Williams (1999: $\chi^2 = 82.2$, $df = 19$, $P < 0.0001$; 2000: $\chi^2 = 94.9$, $df = 19$, $P < 0.0001$). Nests in both forests differed from controls by having denser vegetation (primarily woody *Rubus* spp. stems, but also some herbaceous cover) at the lowest level above the ground, and fewer total tree stems per hectare. In South Walsingham, nests also had denser vegetation at the other three levels above the ground, more snags

Table 1. Habitat variables for hooded warbler (*Wilsonia citrina*) nest and control sites in St. Williams and South Walsingham.

Variable	St. Williams						South Walsingham			
	Nests in 1999 (24)		Nests in 2000 (33)		Controls (41)		Nests (52)		Controls (66)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Coniferous stems (%)	49.6	5.6	53.6	4.9	52.7	4.7	10.3	2.2	12.4	2.5
Coniferous basal area (%)	67.8	5.9	63.0	5.2	56.8	5.4	11.2	2.6	14.5	3.0
Canopy height (m)	27.9**	0.7	25.9**	0.4	22.9	0.9	nm			
Distance to nearest trail (m)	40.3	12.5	35.3	5.4	35.9	5.6	nm			
Canopy cover (%)	77.9	3.7	70.0*	3.2	78.0	3.1	74.1	2.0	78.3	1.3
Vegetative cover (%)										
0–0.3 m	90.8**	3.0	91.3**	2.2	78.6	3.3	84.2**	1.8	66.0	2.7
0.3–1 m	68.5	4.5	76.1**	3.7	57.5	3.5	61.8**	2.6	39.6	2.9
1–2 m	40.4	4.7	61.0*	3.9	46.8	4.1	57.9**	3.2	37.1	2.8
2–3 m	34.9	4.9	52.6*	4.2	37.9	3.9	56.2**	2.9	39.5	2.9
Number of tree species per plot	5.8	0.4	5.3	0.3	5.8	0.2	8.8	0.4	8.1	0.3
Tree basal area (m ² /ha)	31.5	2.3	26.8	1.8	30.50	2.0	25.5	1.5	25.8	1.3
Number of stems/ha	614**	39	564**	45	861	50	1005**	63	1319	75
Log basal area (m ² /ha)	0.5	0.3	4.8**	1.0	1.0	0.5	7.3	1.0	6.5	1.0
Number of logs/ha	17	5	139**	25	24	6	469	48	459	33
Snag basal area (m ² /ha)	2.3	0.5	2.3	0.5	1.8	0.3	2.3	0.5	2.0	0.5
Number of snags/ha	89	16	88	12	96	13	105**	14	177	17
Stump basal area (m ² /ha)	9.8**	3.3	18.5**	3.0	3.5	1.3	nm			
Number of stumps/ha	46**	11	93**	14	27	10	nm			
Basal area due to small trees (m ² /ha)	13.0	1.3	13.0	1.5	15.8	1.3	13.3**	1.0	17.3	1.0
Basal area due to large trees (m ² /ha)	18.8	2.3	13.8	1.5	15.0	2.0	12.3**	1.3	8.8	1.3

Note: Numbers in parentheses are sample sizes; "nm" indicates that the variable was not measured. Asterisks indicate *P* values from Wilcoxon's rank-sum tests comparing nests and controls within St. Williams or South Walsingham (*, *P* < 0.05; **, *P* < 0.01).

per hectare, less basal area due to small trees, and greater basal area due to large trees than controls. In St. Williams, nests had higher canopy, more stumps, and more basal area due to stumps than controls (Table 1).

We also compared 2000 nests with 1999 controls in St. Williams to see if the same variables were important in both years. Indeed, the same five variables differed significantly between nests and controls in 2000, but also vegetative density at the other three levels above the ground was significantly higher around nests than around controls, percent canopy cover was significantly lower around nests than around controls, and nests had more logs, and thus more basal area due to logs, than controls (Table 1).

The same three variables (number of tree stems, number of tree species, vegetative density 1–2 m above the ground) entered the logistic regressions comparing nests and controls in both South Walsingham (1995–1997: $Y = -4.82 - 0.03(\text{number of stems}) + 0.21(\text{number of tree species}) + 0.04(\text{vegetative density } 0\text{--}0.3 \text{ m above the ground}) + 0.02(\text{vegetative density } 1\text{--}2 \text{ m above the ground})$) and St. Williams (1999: $Y = -1.03 - 0.19(\text{number of stems}) + 0.67(\text{number of tree species}) + 0.08(\text{vegetative density } 0.3\text{--}1 \text{ m above the ground}) - 0.07(\text{vegetative density } 1\text{--}2 \text{ m above the ground})$). The model correctly classified nests and controls 83% of the time in South Walsingham and 78% of the time in St. Williams. In South Walsingham, vegetative density 0–0.3 m above the ground also entered the model, and in St. Williams, vegetative density 0.3–1 m above the ground entered the model. These two vegetative-density variables were highly correlated between sites within forests ($r = 0.76$ in South Walsingham, $r = 0.67$ in St. Williams), suggesting that vegetative density <1 m above the ground in general discriminated nests from

controls in both forests. The number of tree stems and vegetative density 0.3–1 m above the ground also entered the 2000 St. Williams model, along with the number of logs ($Y = 1.57 + 0.07(\text{number of stems}) - 0.40(\text{number of logs}) - 0.03(\text{vegetative density } 0.3\text{--}1 \text{ m above the ground})$; jackknifed concordance = 85.2%).

In St. Williams, 86% of all nest sites (49/57), compared with only 39% (16/41) of control sites, were located in gaps ($\chi^2 = 25.5$, *df* = 1, *P* < 0.0001). The size of gaps used by hooded warblers in 2000 (43 m², or 0.004 ha) differed significantly from the size of gaps at control sites (157 m², or 0.015 ha), but there was no difference between the size of gaps at nest sites (196 m², or 0.02 ha) and control sites in 1999 (Table 2). Gaps at nest sites were much larger in 1999 than in 2000 (Table 2); these differences are likely a result of either differential vegetation growth (1999 was very dry, while 2000 was very wet), or observer differences, between the two years. Eighty-four percent of all gaps (54/64) were created by harvest (Table 2). We were able to determine the age of 18 nest gaps in 1999, 15 of which were created by harvest. Gap age was 6.2 ± 0.9 years, and ranged from 1 to 13 years. In 2000, gap age was 7.6 ± 0.6 years ($n = 22$, 16 by harvest) and ranged from 4 to 14 years.

Stand type and logging history

In St. Williams, hooded warbler territories were found in coniferous stands in greater numbers than expected by chance in both years (1999: $\chi^2 = 9.6$, *df* = 2, *P* < 0.02; 2000: $\chi^2 = 6.1$, *df* = 2, *P* < 0.05; Table 3). To test our classification of territories based on FRI information, we examined habitat measurements around nest sites for which FRI information was available. The FRI classification was supported by nest

Fig. 1. The greatest volume (m³/ha) of trees was removed from St. Williams in 1993 and 1997, and hooded warblers (*Wilsonia citrina*) began colonizing the forest in 1995. Prior to 1995, St. Williams was surveyed annually for birds and no hooded warblers were noted (J.D.M., unpublished data).

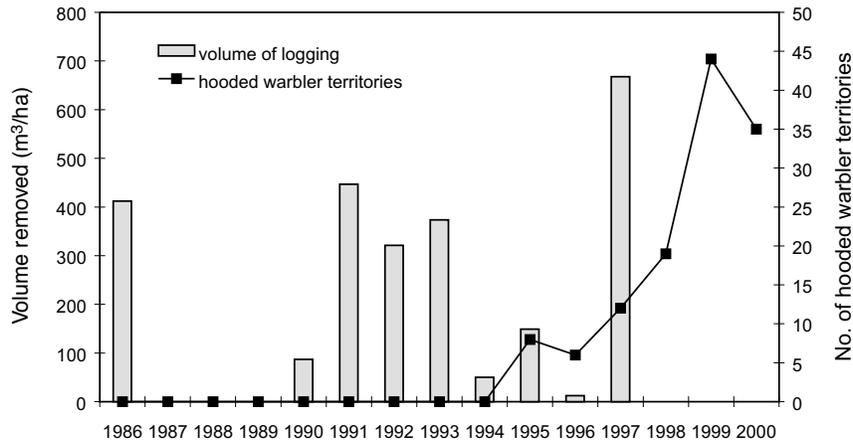


Table 2. Median areas (m²) and interquartile ranges (in parentheses) of gaps associated with hooded warbler nest sites and control sites in St. Williams in 1999 and 2000, organized by method of gap creation.

Method of creation	1999		2000		2000	
	Nest gaps	n	Control gaps	n	Nest gaps	n
Harvest	192 (433)	18	165 (471)	13	43 (62)	23
Windfall	71	1	—	0	35 (71)	3
Dead tree	214 (489)	3	42 (22)	2	—	0
All types combined	196 (422)	22	157 (431)	15	43 (66)	26

Note: Nest gaps were significantly smaller than control gaps in 2000 (Mann–Whitney *U* test, *U* = 200 and *U* = 30, *n* = 10 and *n* = 23, *P* = 0.0009) but not in 1999 (*U* = 125 and *U* = 127; *n* = 12 and *n* = 21; *P* = 0.97). Differences between 1999 and 2000 are likely a result of either differential vegetation growth (1999 was very dry, while 2000 was very wet) or observer differences between the 2 years.

Table 3. Numbers and percentages of hooded warbler territories in stands varying in forest composition in St. Williams in 1999 and 2000, and percentages of the total area of each of these types of habitat available in St. Williams.

Forest type	1999 territories		2000 territories		Area available (%)
	n	%	n	%	
Conifer	19	45.2	11	35.5	29.0
Mixed	20	47.6	18	58.1	45.3
Deciduous	3	7.1	2	6.5	25.8

Note: Habitat use differed significantly from that expected if warblers chose habitat randomly (1999: $\chi^2 = 9.55$, *df* = 2, *p* < 0.02; 2000: $\chi^2 = 6.07$, *df* = 2, *p* < 0.05). The results exclude one territory from 1999 and five territories from 2000 in stands for which FRI data were not available.

measurements, because nests classified as falling into coniferous stands had 79 ± 4% (1999, *n* = 9) and 85 ± 6% (2000, *n* = 10) of total basal area represented by conifers, nests classified as falling into deciduous stands had 0% (1999, *n* = 1, and 2000, *n* = 1) of total basal area represented by conifers, and nests classified as falling into mixed stands had 66 ± 8% (1999, *n* = 10) and 60 ± 7% (2000, *n* = 14) of total basal area represented by conifers.

The greatest volume of logging in St. Williams occurred in 1991 and 1997, and hooded warblers began colonizing the forest in 1995 (Fig. 1). Hooded warbler territories were found in stands of low, moderate, and high logging intensity in

Table 4. Numbers and percentages of hooded warbler territories in stands varying in logging intensity in St. Williams in 1999 and 2000, and percentages of the total area of each of these types of habitat available in St. Williams.

Volume removed (m ³ /ha)	1999 territories		2000 territories		Area available (%)
	n	%	n	%	
0	9	21.4	6	18.2	48.2
0–50	17	40.5	16	48.5	32.2
51–100	8	19.0	7	21.2	10.8
>100	8	19.0	4	12.1	8.8

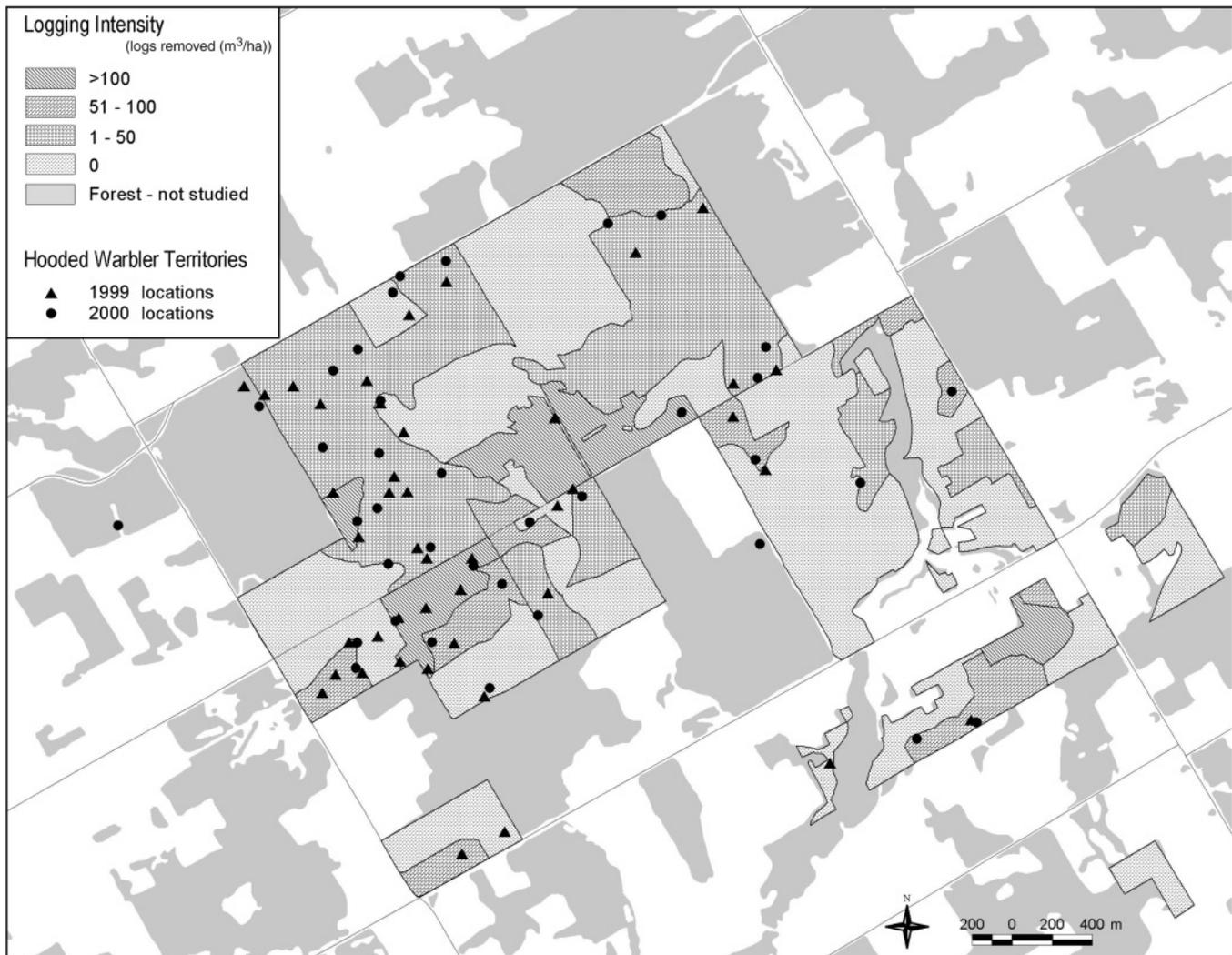
Note: Habitat use differed significantly from that expected if warblers chose habitat randomly (1999: $\chi^2 = 14.81$, *df* = 3, *P* < 0.005; 2000: $\chi^2 = 12.63$, *df* = 3, *P* < 0.005). The results exclude one territory from 1999 and five territories from 2000 in stands for which FRI data were not available.

greater numbers than expected by chance in both 1999 and 2000 (Table 4, Fig. 2; 1999: $\chi^2 = 14.8$, *df* = 3, *P* < 0.005; 2000: $\chi^2 = 12.6$, *df* = 3, *P* < 0.005).

Productivity

In St. Williams we were able to determine the productivity of 21/24 nests (87.5%) in 1999 and 33/33 nests (100%) in 2000. In 1999, 11/21 nests (52%) were parasitized by

Fig. 2. Hooded warbler territories in St. Williams in 1999 and 2000 were found in logged stands more often than expected by chance. Territories were defined as either nest locations or, in cases where nests were not found, the most common perch of singing males.



cowbirds, compared with 13/33 nests (39%) in 2000 ($\chi^2 = 0.9$, $df = 1$, $P = 0.35$). The number of cowbird eggs per parasitized nest was 1.36 ± 0.15 in 1999 and 1.18 ± 0.12 in 2000. There was no significant difference in the number of nests lost during incubation (5/21 in 1999 and 11/33 in 2000) and the chick stage (7/17 in 1999 and 5/22 in 2000; 1999: $\chi^2 = 1.3$, $df = 1$, $P = 0.25$; 2000: $\chi^2 = 0.7$, $df = 1$, $P = 0.40$), so we combined data from the two periods when calculating survival rate and nest success.

Overall productivity (number of young per nest surviving to 5 days of age and daily survival and nest-success rates) of hooded warblers in St. Williams tended to be similar between 1999 and 2000, although more eggs were laid per nest in 2000 (Table 5). Success tended to be higher for unparasitized nests than for parasitized nests in both years (Table 5).

Successful nests (one or more young raised to 5 days of age) did not differ from unsuccessful nests in any of the habitat variables measured (Wilcoxon's rank-sum tests, all $P >$

0.05). Similarly, we found no significant habitat differences between nests that were parasitized (at least one cowbird egg) and those that were not.

Discussion

Hooded warblers consistently chose nest sites with denser vegetation, especially within 1 m of the ground, compared with control sites, regardless of whether they nested in pine or deciduous forest. Other studies from varying forest types in Maryland (Robbins et al. 1989), South Carolina (Hamel 1980⁵; Kilgo et al. 1996; Hazler 1999), Ohio (Petit 1988), Virginia (Crawford et al. 1981), and southwestern Ontario (Bisson and Stutchbury 2000) have also shown that hooded warbler nest sites are characterized by dense understory. It is not known why densely vegetated sites are used, although it may be related to protection from nest predators (although in a study designed to test this possibility, no relationship was

⁵P.B. Hamel. 1980. Guidelines for management of wood warblers (Parulidae) on the Francis Marion National Forest. Unpublished report to the USDA Forest Service, Francis Marion and Sumter National Forests, Columbia, S.C. [Available from P.B. Hamel, 4931 Broad River Road, Columbia, SC 29212-3530, U.S.A.]

Table 5. Nest success of hooded warblers in St. Williams in 1999 and 2000.

	Parasitized nests		Unparasitized nests		All nests	
	1999	2000	1999	2000	1999	2000
No. of eggs/nest	2.27 ± 0.33 (11)	3.25 ± 0.22 (12)	3.40 ± 0.16 (10)	3.6 ± 0.18 (20)	2.81 ± 0.23 (21)	3.47 ± 0.14 (32)
No. of eggs hatched/nest	1.10 ± 0.35 (11)	1.38 ± 0.35 (13)	3.10 ± 0.38 (10)	2.4 ± 0.42 (20)	2.10 ± 0.34 (21)	1.97 ± 0.32 (32)
No. of young surviving to 5 days/nest	0.55 ± 0.31 (11)	0.92 ± 0.35 (13)	2.10 ± 0.53 (10)	1.5 ± 0.41 (20)	1.29 ± 0.34 (21)	1.27 ± 0.28 (33)
Daily survival rate	0.905 ± 0.032 (9)	0.950 ± 0.020 (12)	0.969 ± 0.018 (8)	0.940 ± 0.018 (17)	0.936 ± 0.019 (17)	0.944 ± 0.014 (29)
95% CL	0.842–0.968	0.910–0.989	0.934–1.004	0.904–0.976	0.899–0.973	0.917–0.971
Nest success	0.182 (9)	0.415 (12)	0.583 (8)	0.350 (17)	0.325 (17)	0.376 (29)
95% CL	0.053–0.570	0.202–0.827	0.313–1.062	0.180–0.663	0.165–0.624	0.231–0.603

Note: Values are given as the mean ± SE. Numbers in parentheses are sample sizes; CL, confidence limits.

found; Howlett and Stutchbury 1996), provision of a warm microclimate, improved foraging opportunities (Smith and Dallman 1996), or protective cover for fledged young.

Crawford et al. (1981) found that hooded warblers were more likely to be found in mature stands with large stems (DBH >36 cm) in the Appalachians, and Bisson and Stutchbury (2000) found fewer small trees around nests than at unoccupied sites in various forest stands (including St. Williams) in southwestern Ontario. However, in the latter study, significantly more large trees were not found around nests than unoccupied sites. The authors concluded that forest maturity within the woodlot may not limit hooded warbler nest sites. Our results suggest the opposite. While not all differences were significant (Table 1), the basal area due to small trees was always less and the basal area due to large trees was usually more around nests than at control sites, indicating that forest maturity within the woodlot is an important factor in nest-site selection by this species. Our sampling plots (0.04 ha) were larger than the average gap size (0.02–0.004 ha), allowing us to detect large trees in or around gaps. The significantly higher canopies around nests than at control sites in St. Williams further support this conclusion. In Bisson and Stutchbury's (2000) study, control sites were chosen by walking 150 m in a cardinal direction from an occupied hooded warbler nest site. It is therefore likely that many control sites were in the same forest stands as nest sites. Given that stands tend to be managed uniformly, differences in habitat maturity within a stand would be small. However, selection of relatively mature stands by hooded warblers would not have been detected by their sampling method.

Within St. Williams, hooded warblers selected logged sites for nesting. We found more cut stumps and a greater basal area due to cut stumps around nests than at control sites in St. Williams, and nest sites were more likely to be associated with a canopy gap than were control sites. Almost all gaps in St. Williams, whether at a nest or control site, were created by harvest. Finally, when we examined the distribution of hooded warbler territories in stands with varying logging intensities in St. Williams, we found that hooded warbler territories were more likely to be found in logged stands than would be expected by chance.

Selective logging has been found to have a positive influence on the presence of hooded warblers in a number of other cases. Baker and Lacki (1997) found that hooded warblers were more abundant in stands that had undergone "low-leave" cuts (3.5 m² residual basal area per hectare) and "high-leave" cuts (7 m² residual basal area per hectare) than in stands that were not harvested at all. Similarly, Annand and Thompson (1997) found that hooded warblers were more abundant in stands that underwent group and single-tree-selection cuts than in either mature stands or stands that underwent clear-cutting or shelterwood treatments. Furthermore, Rodewald and Smith (1998) found that selective cutting which also involved heavy cutting of understory vegetation (to lower competition and promote regeneration of desirable tree species like oak) was deleterious for hooded warblers, suggesting that the dense shrub and herb layer generated by the canopy opening, rather than the canopy opening itself, is a key habitat feature for this species.

In uncut mature forests, hooded warbler populations are maintained in natural gap habitats that are created by the

periodic death of trees, whether caused by wind damage, disease, or senescence. When used judiciously, selective logging, which generally creates forest openings from 0.02 to 0.4 ha (Smith 1962), can mimic gaps created by natural disturbance. In St. Williams, hooded warblers used gaps of varying sizes, from 5 m² (0.0005 ha) to 1178 m² (0.12 ha), with the median gap size ranging from 0.02 ha in 1999 to 0.004 ha in 2000. The difference in gap size between 1999 and 2000 is likely a result of either differential vegetation growth or observer differences in measurement techniques over the two years. Gaps ranged in age from 1 to 14 years, with a mean gap age of about 7 years. Robinson and Robinson (1999) found that hooded warblers colonized selectively logged sites in a deciduous forest in Illinois 1–4 years after logging, then disappeared. However, hooded warblers can likely be retained for longer periods (and potentially indefinitely) in large forest tracts like St. Williams if harvest regimes are applied in different stands at different times, so that there is an ongoing rotational supply of gaps of various ages over time.

Within St. Williams, hooded warblers were more likely to nest in pine plantations than in mixed or deciduous stands. This is probably a result of greater selective logging in this habitat type rather than a preference for coniferous trees per se. Most recent logging operations in St. Williams have involved thinning or selectively logging the pine plantations; relatively little logging has occurred in deciduous stands. All other studies of habitat selection by hooded warblers (except Hazler 1999) have examined hooded warblers in deciduous or mixed forest, and the species is generally described as inhabiting mixed hardwood forests (Evans Ogden and Stutchbury 1994). Hazler (1999) concluded that loblolly pine (*Pinus taeda*) plantations can maintain viable populations of hooded warblers, provided a substantial deciduous shrub layer is present. The use of selectively logged pine plantations provides an important opportunity for conservation of this species, given that there have been large increases in conifer plantations over the last 25 years in southern Ontario (Riley and Mohr 1994).

The South Walsingham forest has undergone much less logging in recent years than St. Williams, although approximately 12% of the total forest in South Walsingham has experienced some cutting since 1986 (M.E.G., unpublished data). In 2000, all hooded warbler nests found in this forest ($n = 5$; M.E.G., unpublished data) were located in natural gaps as opposed to harvested sites. The hooded warbler population in this forest has been declining over the last 5 years, from a high of 25 pairs in 1995 to a low of 15 pairs in 1999 (although it rebounded slightly in 2000, with up to 18 pairs; M.E.G., unpublished data). There has been a concurrent increase in the number of hooded warblers in St. Williams, from 0 pairs in 1994 to 8 pairs in 1995 (Wallace and McCracken 1995⁶) to possibly 43 pairs in 1999. Selective logging in St. Williams between 1986 and 1997 appears to have opened up gaps that are suitable for this species, perhaps prompting the local population to shift 6 km from South Walsingham to St. Williams. Several birds banded as nestlings in South Walsingham have been found breeding in

St. Williams, which supports the suggestion that they represent a shift in the same local population. With one exception, however, established adults do not appear to move between the two sites (M.E.G., unpublished data). Alternatively, the population in St. Williams may be increasing concurrently with the entire Ontario population, as increases have been observed in recent years in areas of suitable habitat (M.E.G., unpublished data).

Because the two sites differ in both logging history and forest composition, we are unable to measure the differential effects that forest type and logging intensity might have on hooded warbler occupancy. Given that hooded warblers declined in the lightly logged deciduous forest, increased in the heavily logged coniferous forest, preferentially nested in gaps created by harvest, and made the unusual move of colonizing a pine plantation only after it had been logged, we conclude that this species was responding primarily to forest harvest.

In general, hooded warblers in St. Williams do not appear to be experiencing any more parasitism or nest failure than has been reported for this species at other sites. The rate of parasitism by brown-headed cowbirds (*Molothrus ater*) was higher in St. Williams (39–52%) than at other scattered sites in southwestern Ontario (18%; Bisson and Stutchbury 2000), but was not different from parasitism rates previously noted (1988–1993) in South Walsingham (45%; Evans Ogden and Stutchbury 1994). Furthermore, overall productivity of hooded warblers in St. Williams was similar to that found in other studies. Our daily survival rates of 0.936 (1999) and 0.944 (2000) were similar to those found in loblolly pine plantations in South Carolina (0.933; Hazler 1999) and in bottomland hardwoods (0.941, Sargent et al. 1997), although they were much lower than those reported previously in southwestern Ontario (0.986–0.993, Bisson and Stutchbury 2000; 0.980 in South Walsingham between 1988 and 1993, M.E.G., unpublished data).

Further studies comparing nesting success in logged and unlogged sites could provide a more definitive answer on whether hooded warbler productivity is influenced by the way gaps are created. For example, some studies have shown increased predation and parasitism in selectively logged or thinned forests (e.g., Barber et al. 2001). Interestingly, a study of a small number of hooded warblers nesting in selectively cut areas in Illinois showed that these birds had very low nesting success, with 85% of 13 nests parasitized and a daily predation rate of 8.9% (S.K. Robinson, unpublished data). Because no nests were found at unlogged sites, a comparison between logged and natural sites was not possible; however, hooded warblers are known to have low reproductive success in most parts of Illinois (S.K. Robinson, personal communication).

To benefit hooded warblers, and potentially remove them from Canada's list of Species At Risk, forest managers in southwestern Ontario should practice single-tree- or small-group-selection logging treatments that create gaps no larger than about 0.05 ha (i.e., with a diameter of about 25 m), and should leave the resulting shrub layer untouched. This guideline conforms well with single-tree-selection treatments that

⁶E.H. Wallace and J.D. McCracken. 1995. A survey of the breeding birds of St. Williams Provincial Forest Station. Unpublished report by the Long Point Bird Observatory for the Ontario Ministry of Natural Resources, Port Rowan, Ont.

are typically used when the silvicultural goal is to promote shade-tolerant hardwoods like sugar maple and American beech. By necessity, somewhat larger gaps (0.05–0.20 ha) will be created by group-selection cuts when the goal is to promote regeneration of mid-tolerant hardwoods like oak and pine (OMNR 2000). In such cases, gap size will be at the upper limit of that used by hooded warblers. In large forest blocks exceeding about 100 ha, we recommend that harvest not occur simultaneously across the entire forest, but rather be staggered over a period of several years, and preferably decades, to ensure long-term suitability for hooded warblers.

Managers should retain some mature trees (i.e., DBH >38 cm) at every site because our results have shown that large trees are an important feature of hooded warbler nest sites, providing the appropriate horizontal and vertical habitat structure needed for nesting: a patchwork of shrubby understory in the lowest stratum (required for nesting or for fledged young), combined with a relatively open subcanopy (used for song perches) and a relatively closed upper canopy layer. To this end, we recommend leaving a residual basal area in the large tree size classes of at least 12 m²/ha, as we found that basal area due to large trees varied from 12 to 19 m²/ha depending on the site and year. Even selective logging could be detrimental to gap-dependent forest-interior species such as the hooded warbler if only the most mature trees are selected, as is the case with intensive diameter-limit cuts. Managers of pine plantations should be especially encouraged to follow these guidelines when thinning in order to encourage nesting by hooded warblers.

Finally, when considering the best prescription for a particular woodlot, forest managers should also consider the needs of other at-risk community associates of the hooded warbler, such as the Acadian flycatcher (*Empidonax vireescens*), which is listed as endangered in Canada. While a specified amount of selective logging may benefit hooded warblers, it may be less suitable for Acadian flycatchers, which require a more closed canopy with little ground cover for nesting (Bisson et al. 2000). This provides further argument for the staggering of selective harvest across large forest tracts to ensure that suitable habitat for each of these species is always available.

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