Nest-site characteristics and breeding success of three species of boreal songbirds in western Newfoundland, Canada

Kate L. Dalley, Philip D. Taylor, and Dave Shutler

Abstract: Delineating habitat requirements and preferences of species is essential for conservation planning. We studied nest habitat use and effects of microsite vegetation characteristics on breeding success of yellow-rumped warblers (*Dendroica coronata* (L., 1766)), blackpoll warblers (*Dendroica striata* (J.R. Forster, 1772)), and white-throated sparrows (*Zonotrichia albicollis* (Gmelin, 1789)) in an area with a low extent (<6% of available land) of forest harvest in northwestern Newfoundland. During 2004 and 2005, 99 nests were located and monitored, and the characteristics of nest sites measured. Vegetation at yellow-rumped and blackpoll warbler nest sites differed from random sites; however, within used sites, no vegetation characteristics were significantly associated with success. White-throated sparrow nest sites contained more downed wood and less ground vegetation than did random sites; however, successful nests were associated with different variables than those that distinguished them from random sites, including less canopy cover and less woody debris. Thus, whereas yellow-rumped and blackpoll warblers used specific nest-site characteristics and white-throated sparrows had higher nest success associated with certain characteristics, the nest characteristics these birds appeared to choose did not have demonstrable fitness benefits.

Résumé : La planification de la conservation nécessite une définition des besoins et des préférences d'habitat des espèces. Nous étudions l'utilisation de l'habitat de nidification et les effets des caractéristiques de la végétation à l'échelle du microsite sur le succès de la reproduction chez la paruline à croupion jaune (*Dendroica coronata* (L., 1766)), la paruline rayée (*Dendroica striata* (J.R. Forster, 1772)) et le bruant à gorge blanche (*Zonotrichia albicollis* (Gmelin, 1789)) dans une région à coupe forestière limitée (<6 % des terres disponibles) dans le nord-ouest de Terre-Neuve. En 2004 et 2005, nous avons identifié et suivi 99 nids et mesuré les caractéristiques des sites de nidification. La végétation aux sites de nidification de la paruline à croupion jaune et de la paruline rayée diffère de celle de sites choisis au hasard; cependant au sein même des sites utilisés, aucune caractéristique de la végétation n'est significativement associée au succès de la reproduction. Les sites de nidification des bruants à gorge blanche contiennent plus de bois au sol et une végétation au sol moins dense que les sites choisis au hasard; cependant, les nids qui ont connu du succès sont associés à des variables différentes de celles qui les distinguent des sites aléatoires, en particulier une canopée moins fermée et moins de débris ligneux. Ainsi, alors que les parulines à croupion jaune et les parulines rayées utilisent des caractéristiques spécifiques du site de nidification et les bruants à gorge blanche ont une nidification mieux réussie en présence de certaines particularités, les caractéristiques du nid que ces oiseaux semblent sélectionner ne possèdent pas d'avantages démontrables pour la fitness.

[Traduit par la Rédaction]

Introduction

Organisms are rarely distributed randomly in time or space, and patterns in habitat use are presumed to be the consequence of natural selection (Southwood 1977; Clark and Shutler 1999). Avian nest-site choice is often under intense selection because of the risks of predation (Ricklefs 1969; Martin and Roper 1988; Lloyd and Martin 2004). Other important factors include accessibility of food and shelter from weather (Dawson et al. 2005; Smith et al. 2005; Tremblay et al. 2005). Collectively, these influences have been identified as causes of nonrandom nest habitat use in many taxa of birds (Colwell and Oring 1990; Gloutney and Clark 1997; Davis 2005).

Delineating nest-site preferences is one approach to understanding how songbird populations are influenced by changes in habitat. Such information can also be used for management, because identifying the features of the surrounding environment that are linked to successful nesting, and determining how these features influence success, increases our understanding of specific habitat needs (Warkentin et al. 2004). Such knowledge is particularly important for boreal forest songbirds, for which there is a paucity of basic information, and where large-scale changes in habitat are occurring.

Nest-site habitat can be described by comparing used to unused nest habitats, and because birds may be relegated to marginal nest habitat (Wiens and Rotenberry 1981; Van Horne 1983), it is also important to compare habitats of successful nests with habitats of unsuccessful nests (Clark

K.L. Dalley, P.D. Taylor, and D. Shutler.[1] Acadia University, Department of Biology, Atlantic Cooperative Wildlife and Ecology Research Network, Wolfville, NS B4P 2R6, Canada.

[1]Corresponding author (e-mail: dave.shutler@acadiau.ca).

and Shutler 1999). We assessed both measures for breeding songbirds inhabiting boreal forest with a low extent of harvest in western Newfoundland, Canada. We first tested for nonrandom nest habitat selection by comparing structural characteristics at nest sites and random sites. We then tested whether these characteristics were important to nest success by comparing successful nests with nests that failed because of predation, abandonment, or poor construction. Finally, to make our results comparable with previous studies, we also tested if nest-site characteristics differed between successful nests and only those that were depredated. We hypothesized that there would be species-specific nonrandom nest habitat use. We also hypothesized that structural characteristics that were apparently preferred for nesting would be associated with higher nest success.

Materials and methods

Study area

The study occurred in western Newfoundland, Canada, in the Main River watershed of the Gros Morne Greater Ecosystem (Fig. 1; UTM: 479000 m east, 5514000 m north). The majority of the island of Newfoundland is dominated by tracts of continuous second-growth forest remaining from historical timber extraction (Sturtevant et al. 1996) so that most areas are in early successional stages (Thompson 1991). The Main River area encompasses some of the few remaining nonharvested forests in Newfoundland, and is composed of black spruce (*Picea mariana* (P. Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) P. Mill.) (Belanger et al. 2003), as well as scrub, peatlands, and ponds. Parts of the study area were harvested between 1997 and 2001, but operations ceased in 2001, in part to help maintain ecological integrity of the greater ecosystem of Gros Morne and the Main River UNESCO world heritage site. The extent of harvest (5.9% of the landscape) is considerably lower than that of other managed boreal forests (Whitaker et al. 2008). Harvesting left riparian buffer strips, unmerchantable tree patches, and dead woody debris in the landscape, as well as patches of unharvested timber.

We identified three replicate pairs consisting of one natural landscape of heterogeneous habitat (as described above) coupled with a similar landscape that also contained openings from partial harvests that had occurred in 1999 and 2000. Each of these six study areas was approximately 2 km × 2 km (Fig. 1).

Field methods and study species

Between early June and late July 2004 and 2005, nests were located and monitored in sample landscapes (Fig. 1). General nest-searching methods followed Ralph et al. (1993) and entailed observing adult behaviour and flushing brooding females while searching suitable habitat. We attempted to locate nests of any breeding species that we encountered, and we acquired sufficient data (i.e., >25 nests) for detailed analyses on yellow-rumped warblers (*Dendroica coronata* (L., 1766)), blackpoll warblers (*Dendroica striata* (J.R. Forster, 1772)), and white-throated sparrows (*Zonotrichia albicollis* (Gmelin, 1789)) (Dalley 2007). Each of these common Canadian boreal species builds an open cup nest consisting of small twigs, rootlets, and mosses

Fig. 1. General location of study area (solid box in Newfoundland, Canada), and location of study landscapes outside Gros Morne National Park (●). Partially harvested sites (harv1–harv3) were paired with unharvested (nat1–nat3) sites.
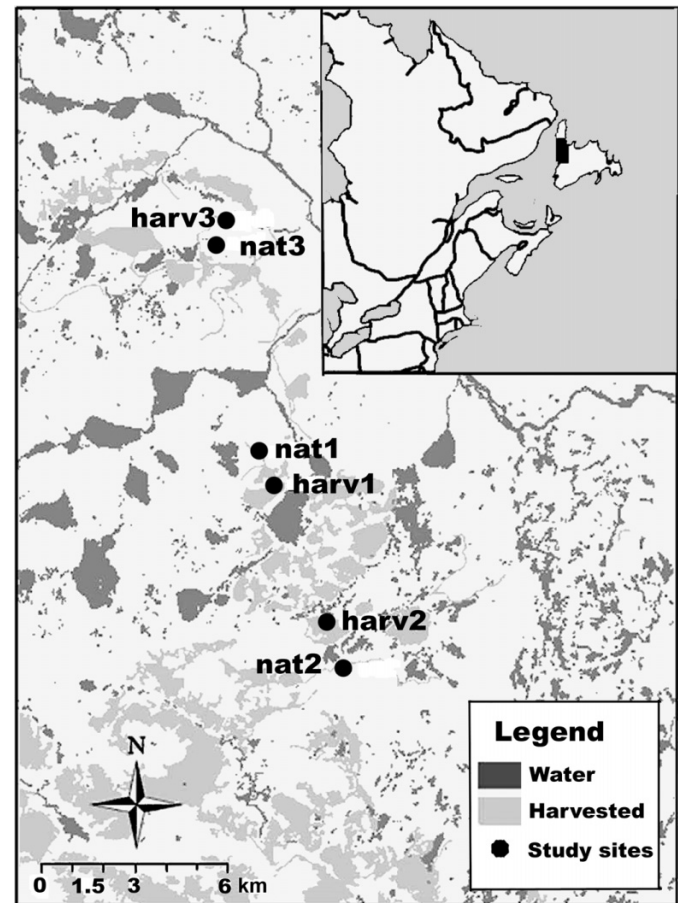
lined with grasses and feathers (Ehrlich et al. 1988). The species are territorial and considered socially monogamous, with both sexes incubating and feeding young. Yellow-rumped warblers breed predominantly in coniferous forests in nests situated >1 m above ground. Blackpoll warblers breed in coniferous scrub and forests, generally within 1 m of the ground. White-throated sparrows nest at ground level along edges and in openings of coniferous forests (Ehrlich et al. 1988). Information on nest-site habitats for these species is limited. Most knowledge of yellow-rumped warbler and white-throated sparrow nest habitats comes from broad community analyses (Falls and Kopachena 1994; Hunt and Flaspohler 1998), whereas our knowledge regarding blackpoll warbler nest habitats is limited to Kent Island, New Brunswick, and New Hampshire (Sabo 1980; Eliason 1986; Hunt and Eliason 1999). In western Newfoundland, mammals are believed to be the main predators of songbirds, based on studies of artificial ground nests (Lewis and Montevecchi 1999).

When nests were found, nest stage and contents were recorded. Nests were subsequently visited every 3 days to check their contents. To minimize human-induced mortality, nests were approached and vacated from different directions to avoid leaving dead-end trails (Martin and Geupel 1993). Poles with mirrors were used to view nests that were diffi-

Table 1. Characteristics measured to compare used to unused sites, successful to unsuccessful nests, and successful to depredated nests.

Nest-site characteristics	Mnemonic	Description
Concealment	conc.	A measure of how covered the nest is. This is measured as a whole number from 1 to 8, indicating the number of 8 pie pieces visible on a 7.3 cm diameter disc placed in the nest. Observations were taken from 1 m directly above and 1 m above and beside the nest in each cardinal direction
Canopy opening	can.open	A continuous variable describing the number of visible dots observed. Reported values are the mean number of dots collected while standing at the nest, holding a densitometer at elbow height, and facing each of four cardinal directions. Higher values indicate that a site has less canopy cover
Small downed wood	smDW	The mean number of downed wood >1 m and <10 cm in diameter found along transects in each cardinal direction within a given radius of the nest collected at 0–1 and 1–5 m from the nest
Large downed wood	lgDW	The mean number of downed wood >10 cm in diameter found along transects in each cardinal direction within a given radius of the nest collected at 0–1 and 1–5 m from the nest
Ground cover (GC)		Defined as any ground cover <0.5 m high collected at 0–1 and 1–5 m from the nest
GC water	h2o	A proportion measure of ground cover collected at 0–1 and 1–5 m from the nest. Water includes puddles, ponds, streams, and wet bogs
GC coarse woody debris	Cwd	A proportion measure of ground cover collected at 0–1 and 1–5 m from the nest. Coarse woody debris includes dead or rotting logs, stumps, and branches
GC bare ground	Bare	A proportion measure of ground cover collected at 0–1 and 1–5 m from the nest. Bare ground includes rock, gravel, and soil
GC low vegetation	Lv	A proportion measure of ground cover collected at 0–1 and 1–5 m from the nest. Low vegetation includes any herbaceous vegetation <10 cm high
GC high vegetation	hg	A proportion measure of ground cover collected at 0–1 and 1–5 m from the nest. High vegetation includes any herbaceous vegetation >10 cm high
GC tree	Tree	A proportion measure of ground cover collected at 0–1 and 1–5 m from the nest. Trees include woody stems having parts <0.5 m high
Stems <1 m	stems.1	A count of woody stems <1 m high collected at 0–1 and 1–5 m from the nest
Stems 1–2 m	stems1.2	A count of woody stems 1–2 m high collected at 0–1 and 1–5 m from the nest
Stems >2 m	stems2	A count of woody stems >2 m high collected at 0–1 and 1–5 m from the nest

cult to approach or that were too high to observe directly. In most cases, visual or auditory observations of fledglings with adults were used to determine if a nest was successful.

After nests successfully fledged one or more young, or failed, microsite structural vegetation data (Table 1) were collected. Circular plots extending from the nest (Larison et al. 1998) were divided into quadrants using the four cardinal directions as boundaries. Data were collected within 1 and 5 m radii around the nest and averaged from the four quadrants. To assess nest-site selection, nest-site variables were also collected from a single random nest site located in a randomly chosen direction 20 m from the used site. Appropriate nest placement (nest height and nest substrate) options were not necessarily available at random sites and thus do not appear in analyses of nest site versus control sites.

We did not observe birds actively choosing nest sites, and therefore did not actively assess avian habitat selection. Thus, although nonrandom habitat use implies that there was "selection", we prefer to use the term "use" when describing nest placement.

Statistical analyses

All statistical analyses were conducted using R version 2.4.0 (R Development Core Team 2006). To determine which habitat variables best discriminated used from random, successful from all unsuccessful (all causes of failure), and successful from depredated sites, we used logistic regression. Logistic regression is suitable for studies (such as this one) that employ case-control sampling. Because the proportion of habitat occupied by nests is tiny, a control or unused site is sampled for each used site (Keating and Cherry 2004). An underlying assumption is that random sites are indeed unused.

We assessed predictor variables for multicollinearity. Low vegetation (lv), high vegetation (hv), and tree (tree) cover classes of ground cover were highly correlated (Kendall's $\tau \geq 0.40$), so we included only hv in the model selection process. We log-transformed variables that were not normally distributed and converted to binomial some continuous variables that included >50% zeros. Final decisions regarding which structure of predictor variables to include in the full model were made based on model fit (patterns of distribution of residuals and quality of parameter estimates).

To determine which predictor variables were included in the final model, we used a modified backwards selection approach. We initially fit all main effects. If we were unable to fit all main effects (because of model convergence problems), we fit univariate models and included only significant terms in a reduced full model. Predictors with the highest P values and contributing the least to overall model deviance were eliminated from the model first. When a candidate model included only parameters that were significantly different from zero (t test, maximum probability of a type I

Table 2. Number of nests of yellow-rumped warblers (*Dendroica coronata*), blackpoll warblers (*Dendroica striata*), and white-throated sparrows (*Zonotrichia albicollis*) located on a given substrate type and in a given height class.

| | Nest substrate | | | | | | Nest height (m) | | | | | | |
	Balsam fir (*Abies balsamea*)	Black spruce (*Picea mariana*)	Moss	Bare	Snag	Other	0	0.1–0.5	0.6–1.0	1.1–1.5	1.6–2.0	2.1–6.0	6.1–12.0
Yellow-rumped warbler	16	9	0	0	2	0	0	2	4	3	2	8	7
Blackpoll warbler	17	12	4	2	2	2	7	21	10	0	1	0	0
White-throated sparrow	1	0	25	6	0	1	32	1	0	0	0	0	0

Table 3. Results of logistic regression models for yellow-rumped warblers (*Dendroica coronata*), blackpoll warbles (*Dendroica striata*), and white-throated sparrows (*Zonotrichia albicollis*) comparing nests to random sites, successful nests to failed nests (from abandonment or depredation), and successful nests to depredated nests.

| | Nest vs. random (1 m) | | | Nest vs. random (5 m) | | | Success vs. fail (1 m) | | | Success vs. fail (5 m) | | | Success vs. depredated (1 m) | | |
Variable	β	SE	P	β	SE	P	β	SE	P	β	SE	P	β	SE	P
Yellow-rumped warbler															
can.open	—	—	—	–0.04	0.01	<0.01	—	—	—	—	—	—	—	—	—
lgDW	2.97	1.14	<0.01	—	—	—	—	—	—	—	—	—	—	—	—
Hv	—	—	—	—	—	—	—	—	—	–0.26	0.15	0.07	—	—	—
stems1.2	5.85	2.68	0.03	1.44	0.67	0.03	—	—	—	—	—	—	—	—	—
stems.2	5.80	1.80	<0.01	–0.31	0.15	0.04	—	—	—	—	—	—	—	—	—
Blackpoll warbler															
lgDW	—	—	—	—	—	—	—	—	—	1.70	0.99	0.08	1.68	1.09	0.12
Cwd	0.04	0.02	0.06	—	—	—	—	—	—	—	—	—	—	—	—
Hv	–0.14	0.06	0.02	—	—	—	—	—	—	—	—	—	—	—	—
stems1.2	2.34	0.86	<0.01	0.19	0.07	0.01	—	—	—	—	—	—	—	—	—
stems.2	3.63	1.85	0.05	—	—	—	—	—	—	—	—	—	—	—	—
White-throated sparrow															
can.open	—	—	—	—	—	—	0.06	0.03	0.04	0.07	0.03	0.03	0.12	0.06	0.05
smDW	2.52	0.90	<0.01	—	—	—	–0.54	0.26	0.04	–0.15	0.06	0.02	—	—	—
lgDW	—	—	—	—	—	—	—	—	—	—	—	—	–7.76	4.06	0.06
Cwd	—	—	—	—	—	—	—	—	—	—	—	—	2.90	1.68	0.08
Hv	–0.26	0.07	<0.01	—	—	—	—	—	—	—	—	—	—	—	—

Note: The sign of parameter estimates indicate whether nest sites or successful nests had more or less of a value than random or unsuccessful sites. Only terms in the final model are presented. No nest-site characteristics significantly differentiated successful from failed nests at the 1 m scale or successful from depredated nests at either the 1 or 5 m scales. Marginally significant parameter estimates contributed significantly to the overall model deviance (Fig. 3). For a description of the variables see Table 1.

error = 0.05 = P) and marginally significantly different from zero (0.05 < P < 0.10), models with and without marginally significant terms were compared to see if those terms contributed significantly to reducing model deviance (F or χ^2 test, where appropriate). If it did not, the marginal term was removed and we proceeded likewise until the model included only significant terms and terms that contributed significantly to overall deviance (Crawley 2005).

We used the above methods to determine (*i*) if nest sites differed from random sites, (*ii*) if successful nest sites differed from unsuccessful nest sites (including failures by all causes), and (*iii*) if successful nest sites differed from depredated nest sites. All values are reported as means ± SD and parameters are reported ±SE.

Results

Over the 2 years, we found and monitored nests of 27 yellow-rumped warblers, 39 blackpoll warblers, and 33 white-throated sparrows. Yellow-rumped warbler nest heights were 4.0 ± 3.5 m (range 0.5–12.0 m) and were situated primarily in balsam fir and black spruce trees (Table 2). Blackpoll warbler nest heights were 0.4 ± 0.4 m (range 0.0–2.0 m) and were also usually placed in balsam fir and black spruce trees. All but one white-throated sparrow nest were placed on the ground and moss was the substrate for 76% of nests (Table 2).

Compared with unused sites, yellow-rumped warbler nest sites had more vegetation variables that were associated with natural or forested areas. They had significantly more large downed wood and more stems that were 1–2 m tall and >2 m tall within a 1 m radius of the nest (Table 3, Fig. 2). Within a 5 m radius, nest sites had more canopy cover, more stems 1–2 m tall, and fewer stems >2 m tall than unused sites (Table 3, Fig. 2). Blackpoll warbler nest sites were associated with a mixture of habitat types. They had more coarse woody debris, stems 1–2 m tall and >2 m tall, and less high vegetation ground cover within a 1 m radius of the nest compared with unused sites (Table 3, Fig. 3). Within a 5 m radius, they had more stems 1–2 m

Fig. 2. Box plots of significant predictors of yellow-rumped warbler (*Dendroica coronata*) nest sites (for mnemonics see Table 1). The horizontal bar in the middle indicates the median *y* values and the box contains the middle 50% of all data. Whiskers show the range of data and the points beyond the whiskers indicate outliers. Significant predictors of nest placement within 1 m were (A) large downed wood, (B) stems 1–2 m tall, and (C) stems >2 m tall. Significant predictors of nest placement within 5 m were (D) amount of open canopy, (E) stems 1–2 m tall, and (F) stems >2 m tall.
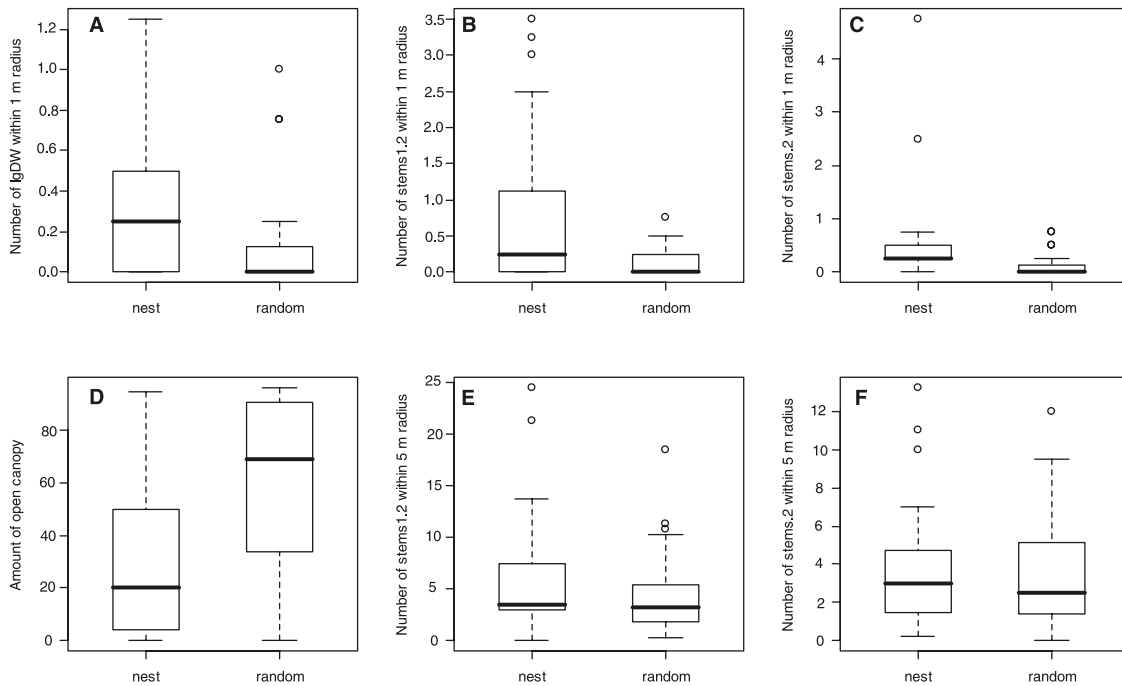
Fig. 3. Box plots of significant predictors of blackpoll warbler (*Dendroica striata*) nest sites (for mnemonics see Table 1). The horizontal bar in the middle indicates the median *y* values and the box contains the middle 50% of all data. Whiskers show the range of data and the points beyond the whiskers indicate outliers. Significant predictors of nest placement within 1 m were (A) high vegetation ground cover, (B) stems 1–2 m tall, and (C) stems >2 m tall. The significant predictor of nest placement within 5 m was (D) stems 1–2 m tall.
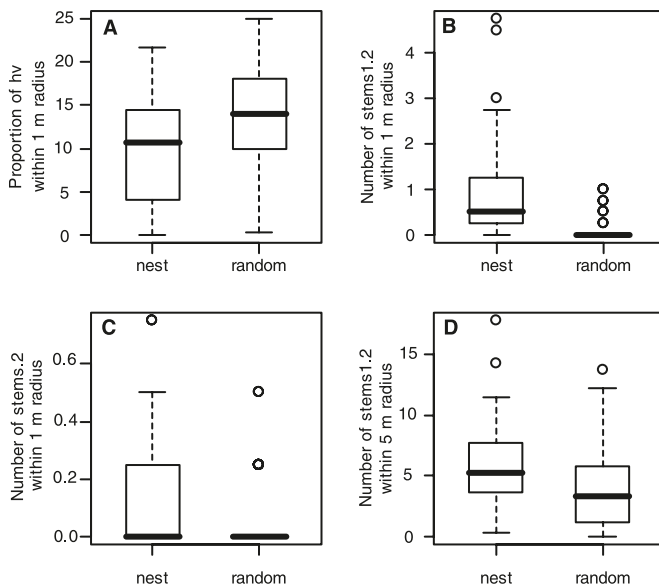

tall than unused sites (Table 3, Fig. 3). Finally, white-throated sparrow nest sites were associated with characteristics more often seen in open and harvested areas. They had more small downed wood and less high vegetation ground cover within a 1 m radius of the nest (Table 3, Fig. 4), and within a 5 m radius, their nest sites did not differ from unused sites.

Eight of nine yellow-rumped warbler, seven of nine blackpoll warbler, and four of six white-throated sparrow nest failures were due to predation. Four nest failures were caused by abandonment (which may occur if one parent dies), and the one yellow-rumped warbler nest failure was caused by nest collapse (it was built on a piece of bark that was loosely attached to a snag). Successful yellow-rumped warbler nests had, within a 5 m radius, less high vegetation ground cover than did unsuccessful nests (Table 3). Successful blackpoll warbler nests had, within a 5 m radius, more large downed wood than did unsuccessful nests (Table 3). Successful white-throated sparrow nests had, within both 1 and 5 m radii, more open canopy cover and less small downed wood than did unsuccessful nests (Table 3, Fig. 4).

For yellow-rumped and blackpoll warblers, successful nest sites did not differ within a 1 or 5 m radius from those that failed because of predation; however, for blackpoll warblers, successful nests had more large downed wood within a 5 m radius (χ^2 test, $P < 0.04$) than did depredated nests. Successful white-throated sparrow nests had less canopy cover, less small downed wood, and more coarse woody debris within 1 m than did nests that failed because of predation (Table 3, Fig. 4), and within a 5 m radius did not differ in habitat from nests that failed because of predation.

Fig. 4. Box plots of significant predictors of white-throated sparrow (*Zonotrichia albicollis*) nest sites and nest success (for mnemonics see Table 1). The horizontal bar in the middle indicates the median *y* values and the box indicates the middle 50% of all data. Whiskers show the range of data and the points beyond the whiskers indicate outliers. Significant predictors of nest placement within 1 m were (A) small downed wood and (B) high vegetation ground cover. Significant predictors of nest success within 1 m were (C) amount of open canopy and (D) small downed wood. Significant predictors of nest success within 5 m were (C) amount of open canopy (same as the measure within 1 m) and (E) small downed wood. The significant predictor of nest success (predation only) was (F) amount of open canopy.
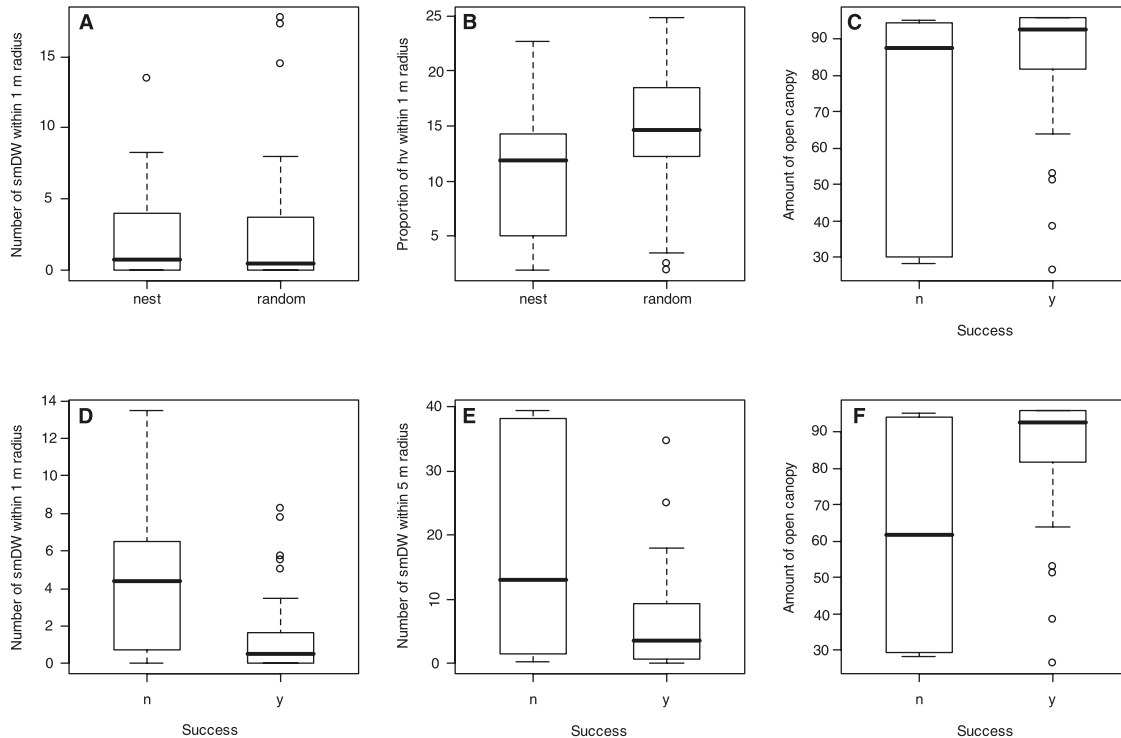
Discussion

Compared with other warblers, yellow-rumped warblers are considered ecological generalists; however, they are largely confined to coniferous forests for breeding (Hunt and Flaspohler 1998). Within coniferous forests, little habitat specificity has been identified (Franzreb 1978; Noon et al. 1980; Douglas et al. 1992). This study is one of few to look at differences between yellow-rumped warbler nest-site use and random sites. Consistent with Clark et al. (1983), nest sites had fewer openings and were located in areas with denser understory (stems 1–2 m tall). Stems >2 m tall and large downed wood were important predictors of nest placement, and both of these attributes are common in forests in the study area.

Blackpoll warblers are a species of northern spruce forest. Our study reiterates the importance of spruce and balsam fir trees as substrates for blackpoll warbler nests (Sabo 1980; Eliason 1986). Although we did not measure canopy height or foliage volume, a related measure (i.e., canopy cover) was not an important variable in distinguishing nest sites from random sites, contrary to Sabo (1980). We found that variables within 1 m were more important than variables at 5 m for nest placement, and these were indicative of habitat that is both open (more coarse woody debris, but less vegetation >10 cm) and forested, with more stems 1–2 m and >2 m tall.

White-throated sparrows prefer forests with numerous openings, with low dense vegetation such as cutover land,

second growth, and open woods (Peters and Burleigh 1951; Falls and Kopachena 1994). Nest habitats are typified by low canopy volume and tree density, dense understory, and increased edge within a 3 m radius of the nest (Clark et al. 1983). Similarly, we found that white-throated sparrows used nest sites with variables that are associated with open areas.

Structural obstacles (small and large downed wood, and coarse woody debris) were more common at nests than at random sites for all three species, and presence of woody stems >1 m tall distinguished used from unused nest sites for the aboveground nesters, yellow-rumped and blackpoll warblers. Tall vegetation was denser at random sites than at nest sites for both blackpoll warblers and white-throated sparrows. This is surprising, as these species tend to nest in transitional and edge habitats that are conducive to growth of ground vegetation. The result suggests that although tall vegetation is found within the territory (at the random site) and is characteristic of the nest at a larger scale, it is not specifically selected for at the nest microsite. The canopy was less open at nest sites than random sites for yellow-rumped warblers. Although this finding supports classifying this species as a forest-nester, this variable did not have a direct influence on nesting success. For the open-nesting white-throated sparrow, our results did not indicate use of more open canopy; however, success was associated with less canopy cover. Other reasons these species nested where they did could include availability of nest material, suitable microclimates, food, and mates. However, birds may per-

ceive anthropogenically modified habitats to be better than they actually are (i.e., ecological traps; Gates and Gysel 1978).

Although we did observe species-specific nest-site placement as we had predicted, contrary to what we hypothesized, none of the species had higher nest success associated with nest-site structural characteristics. The two warblers had more variables associated with nest-site placement than with success, whereas white-throated sparrows had more variables associated with success than with nest-site placement. It is possible that white-throated sparrows used nest sites to avoid nest predation, whereas yellow-rumped and blackpoll warblers used nest sites for other, unmeasured reasons. Alternatively, predators of the warbler nests may search for nests using cues such as parental activity, auditory cues (Skutch 1949; Perrins 1965; Willis 1973), or olfactory cues (Henry 1969; Lill 1974; Reitsma et al. 1990), whereas predators of the ground-nesting white-throated sparrows may be more visually oriented and so are more easily thwarted by vegetation concealment.

We focused mostly on vegetation structure, but plant species composition may also have affected nest-site use and success (MacArthur and MacArthur 1961; Franzreb 1978). In addition, we measured nest-site characteristics following breeding, whereas deciduous vegetation may not emerge until after territories are established, eggs are laid, or even after eggs have hatched. Thus, choices made by birds in establishing territories may be based on permanent structural characteristics or on other knowledge of the breeding area including information gathered from previous years (Doligez et al. 2002). Moreover, processes at larger scales could be more important in influencing nest-site placement than those at the microscale that we considered (Urban and Smith 1989; Braden 1999).

Although nonrandom nest-site use has been reported for many bird species, apparently preferred habitat is not always associated with higher nest success (Filliater et al. 1994; Bisson and Stutchbury 2000; Chase 2002). Fitness benefits of nest-site placement may be difficult to detect for several reasons. In our case, the comparatively high nest success of >67% for each species may mean that the intensity of selection on site placement in Newfoundland is lower than it is in the majority of their breeding ranges. This may increase the importance of other factors to nest-site placement, such as micro- and macro-climate and food availability that influence long-term adult strategies rather than short-term nest placement strategies (Holway 1991; Schmidt 1999; Fontaine and Martin 2006). Stochastic variation in each of the variables that influence nest success (e.g., predation; Devenport and Devenport 1994; Howlett and Stutchbury 1996; Schmidt and Whelan 1999) may mean that nest-site placement reflects average optima from time intervals longer than the 2 years over which we collected data. Proximately, all of these factors may similarly make it difficult for birds to make the best choices.

Low levels of forest harvest appeared to have limited influence on nest-site use and nest success for the three species that we monitored. Whether this is due to resilience of these species to management (Schmiegelow et al. 1997; Leonard 2007; Whitaker et al. 2008), or because effects of this low level of harvest are overwhelmed by other factors

(e.g., weather), is not clear. Moreover, harvest may exert influences at other temporal or spatial scales that we did not consider. Thus, we caution against generalizing these findings to other levels of harvest, and especially to other species. Nonetheless, our study provides valuable data about nesting habitat for three common species of passerines, and indicates structural features that could be retained to favour those species. However, translating these results into optimal conservation investments even for other common species will be more challenging. This translation will be even more difficult for rare and endangered species, in part because of the problems in obtaining sufficient samples sizes to delineate habitat needs (Clark and Shutler 1999).

Acknowledgements

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