

Nest-site selection in the Canada Warbler (*Wilsonia canadensis*) in central New Hampshire

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Abstract: Reproductive success in birds is largely influenced by nest-site selection. Nest predators are the greatest source of nest failure for most species of birds. Species that nest on the ground may be particularly adapted to maximally conceal nests to reduce the risk of loss to predators. Little is known about nest-site selection in the Canada Warbler (*Wilsonia canadensis* (L., 1766)), a small ground-nesting Neotropical migrant. We predicted higher amounts of vegetative cover at successful nests of Canada Warblers compared with unsuccessful nests because detection by predators would decrease with greater cover. We measured vegetative characteristics (concealment, stem densities, ground cover) around each nest and compared these variables between successful and unsuccessful nests and between actual nests and mock nest sites on and off territories. Greater concealment and higher stem densities were the main features surrounding a successful nest site. Nest sites had significantly greater concealment when compared with both random mock nest sites on and off territories. Thus, concealment is important for this ground nester and achieved primarily through thick cover and strategic nest placement in vertical substrate with an inconspicuous opening to the nest cup. Forests with complex ground structure and thickets of small-stemmed woody plants should be targets of conservation when considering how to manage this declining species.

Résumé : Le succès de la reproduction chez les oiseaux est en grande partie influencé par le choix du site de nidification. Pour la plupart des espèces d'oiseaux, les prédateurs des nids sont la source principale d'échecs de la nidification. Les espèces qui nichent au sol peuvent être particulièrement adaptées pour cacher leur nid de manière plus efficace afin de réduire le risque de perte dû aux prédateurs. On connaît mal la sélection du site de nidification chez la paruline du Canada (*Wilsonia canadensis* (L., 1766)), un petit migrateur néotropical qui niche au sol. Nous avons prédit qu'il y a un couvert végétal plus important aux sites de nidification réussie par comparaison aux nids sans succès parce que la détection par les prédateurs devrait diminuer en fonction de l'importance du couvert végétal. Nous avons mesuré les caractéristiques de la végétation (dissimulation, densité des tiges, couverture au sol) autour de chaque nid et comparé ces variables entre les nids réussis et ratés et entre des nids réels et des sites de nidification simulés au sein et hors des territoires. Une dissimulation supérieure et une densité plus élevée de tiges constituent les principales caractéristiques retrouvées autour d'un site de nidification réussie. Les sites de nidification présentent une dissimulation significativement plus élevée par comparaison aux sites de nidification simulés aléatoires, tant à l'intérieur qu'à l'extérieur des territoires. Ainsi, la dissimulation est importante chez ce nidificateur au sol et elle est due principalement à un couvert végétal dense et à la position stratégique du nid dans le substrat vertical avec une ouverture peu apparente menant à la coupe du nid. En considérant la gestion de cette espèce en déclin, on ferait bien de cibler la préservation de forêts qui possèdent une structure complexe au sol et des fourrés de plantes ligneuses à tiges fines.

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Introduction

Selection of both breeding habitats and nest sites affect fitness among individuals within a population and occurs at several spatial scales, including landscape, region, neighborhood, territory, and microsite (Hutto 1985; Jones 2001). Selection of a nest site may be affected by factors such as vegetation type or predator distributions at these different scales (Citta and Lindberg 2007). For example, habitat directly surrounding a nest can influence reproductive success as much as the actual microsite of the nest. Martin (1993) hypothesized that nesting success is greater in a habitat with

a larger number of prospective nest sites because predators cannot confine their search to the few obvious locations. Nest predation has been described in some systems as the greatest source of nest failure (Ricklefs 1968; Rodenhouse 1986; Martin 1992a). Therefore, selection of a nest site that can reduce predation risk would be expected. Concealment may be a nest-site criterion and significant factor in preventing predation (Götmark et al. 1995; however, see Howlett and Stutchbury 1996).

Weidinger (2002) showed ground-nesting Yellowhammers (*Emberiza citrinella* L., 1758) that selected a nest with good concealment had significantly lower amounts of predation

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from corvids, a primary predator of this study's species as well, than higher nesting species such as Eurasian Blackcaps (*Sylvia atricapilla* L., 1758) and thrushes (genus *Turdus* L., 1758). This trend of greater concealment at lower nests is also described by Burhans and Thompson (1998) with low-nesting Field Sparrows (*Spizella pusilla* (A. Wilson, 1810)) that had significantly more concealment than the higher nests of Indigo Buntings (*Passerina cyanea* (L., 1766)) and Northern Cardinals (*Cardinalis cardinalis* (L., 1758)). Other researchers have also found greater concealment surrounding nest sites at lower strata (Stauffer and Best 1980; Murphy 1983; Götmark et al. 1995). Although the physical structure of a nest site is considered to be the main feature for nest-site selection (e.g., MacArthur et al. 1962), it is unlikely to be the only consideration in the selection process. Other features affecting the selection process might include the location of conspecifics (Doligez et al. 2002), prey abundances (Holway 1991), and cover for fledglings (King and DeGraaf 2006).

The Canada Warbler (*Wilsonia canadensis* (L., 1766)), a small (9–12 g) ground-nesting Neotropical migratory passerine, is declining at a rate of 5.2% per year in New Hampshire and 6.4% throughout New England (Sauer et al. 2011), and this decline is not well understood. Nest-site selection plays a significant role in determining reproductive success and no detailed analysis of nest-site selection has been conducted for this species. Presumed higher access for a wider variety of predators to nests of ground-nesting species like the Canada Warbler would select for higher vegetative concealment. We hypothesized greater concealment and more small woody stems around successful nests compared with failed nests. We also hypothesized greater concealment and denser stems around nests compared with simulated nests on and off territories. Preference for areas with dense stems is consistent with a general habitat feature selected by Canada Warblers (Robbins et al. 1989; Sodhi and Paszkowski 1995; Hallworth et al. 2008a, 2008b; Reitsma et al. 2008; Chace et al. 2009) and a feature expected to be accentuated around nests.

Materials and methods

Study site

We conducted this study in Canaan, New Hampshire (43.690, -72.0371). The study area consisted of two plots separated by a 15 ha bog. The plot south of the bog is an interspersed red maple (*Acer rubrum* L.) swamp consisting of red maple, balsam fir (*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sarg.), and mixed upland forest (Hallworth et al. 2008b). The plot north of the bog was heavily logged in 1985 with residual trees left standing. This plot is a mix of early to mid-successional forest consisting primarily of red maple, balsam fir, red spruce, eastern hemlock (*Tsuga canadensis* (L.) Carrière), and various birch species (genus *Betula* L.) interspersed with wet areas similar to the drainages on the lower plot.

Male territories and nest searching

We mapped male territories by marking locations of observed males with global positioning system (GPS) units from 26 May to 10 July 2005–2008. Males were followed until each had a minimum of 42 observation locations recorded as GPS waypoints. Most locations were collected

from sunrise until 0930; however, a small percentage were from observations after 0930. Adaptive kernel (ADK) was used to calculate the territory boundaries (95% ADK) of each male (Barg et al. 2005). The CALHOME home range analysis program was used to calculate territory boundaries (Kie et al. 1996), which were then plotted using ArcMap version 9.3 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA).

Direct searching for nests occurred throughout the nesting cycle and was particularly active during nest-building and nestling-feeding stages. Females carrying nest material were observed from a distance to determine if they returned to the same location. If the building phase was considered too early, a waypoint was taken and searching commenced the next day. If parents were encountered during feeding, we remained motionless and waited for parents to settle down and return to the nest, which could be 10–40 min. Some nests were found by direct searching in areas of ground substrate that appeared highly suitable and a few were found by inadvertently flushing a female from the nest.

Nests found before incubation were viewed at a distance every 3–4 days to determine whether incubation was still occurring. After hatching, these nests and nests found after incubation were visited once at an estimated 2 days prior to fledging so that nestlings were large enough to bleed for paternity analyses (not reported here) and to determine fate of nest to that stage. Each territory was revisited after fledging a sufficient number of times to document whether parents were feeding fledglings. This allowed us to determine reproductive success defined as fledging at least one nestling. In 2007, nests were visited more frequently to record nestling growth rates. We recorded no abandonment resulting from our disturbance.

Nest vegetation plots

Vegetative composition and cover were measured in four 1 m × 3 m belt transects radiating from the nest in each of the cardinal directions. Eleven vegetation characteristics were quantified in each of these transects. These 11 parameters were determined to be of biological importance based on personal observations and previous studies conducted on this population (Hallworth et al. 2008a, 2008b; Reitsma et al. 2008). Percent ground cover was divided into six categories (water, moss, fern stems, leaf litter (abbreviated as LL in models), coarse woody debris (abbreviated as CWD in models), and grass). At the terminus of each transect, we estimated the percentage of the nest that was visible viewing the nest site from 1.5 m off the ground (following part of Weidinger 2002). This height was chosen to standardize and to avoid having the nest be completely obscured, which would have resulted if nest sites were viewed from the ground. The inverse of this estimation of the percentage of the nest visible is the concealment value of the nest (abbreviated to conceal in models). We treated concealment as a vegetative characteristic because vegetation was the primary determinant of how much of the nest was visible. We divided woody stems into three size categories (small: ≤1 m high and ≤1 cm dbh; medium-sized: >1 m high and ≤2.5 cm dbh; large: >1 m high and >2.5 cm dbh). We treated the combination of all three stem categories as a separate variable. In the models described in Table 1, these categories were abbreviated as

smstem, medstem, lgstem, and allstem, respectively. Species composition was not recorded based upon the previous finding that stem density is more important than species composition as a feature selected by this species (Hallworth et al. 2008b). Seven vegetation plots were associated with each nest: 1 at the nest, 2 at randomly selected mock nest sites within the corresponding male's territory, and 3 at randomly selected mock nest sites off males' territories (following Steele 1993; Jones et al. 2001). Mock nest sites were generated on Microsoft Excel and then overlaid on ArcGIS to exclude any locations not on the study site or in irrelevant areas, such as the open water of Bear Pond or other marshes. Mock nest sites off all male territories were positioned outside a 30 m buffer overlaid around all male territories to account for any possible variation in the territory maps. These final points were then uploaded into a GPS to locate the mock nest site. A roll of dark tape approximately 6 cm in diameter (approximately the same size as and used to simulate a nest of a Canada Warbler) was placed on the ground to be used as the center of each vegetation plot. All vegetation measurements were conducted after fledging to avoid disturbance during the active nesting phase.

Statistical analyses

ANOVA was used to determine if year influenced nest success. We also used ANOVA to test whether the mean age of males, the pairing success, or the fledging success differed on the two plots. Age, pairing, and fledging were not different, allowing us to pool the data from both plots on nest sites. Year also did not affect success, allowing us to pool across all 3 years for maximum sample size. Using a pairwise comparison, we compared nest concealment (as measured by percentage of nest visible) between actual nest sites, random mock nest sites on territories, and random mock nest sites off territories with an ANOVA. We conducted a post hoc Bonferroni multiple comparison to determine which factors if any were significantly different. We considered a nest successful if at least one nestling fledged, which was determined by visual confirmation (Howlett and Stutchbury 2003) or adults going to the ground with food in several locations (Hallworth et al. 2008b). We used SPSS version 14.0 (SPSS Inc., Chicago, Illinois, USA) to conduct the ANOVAs.

Akaike's information criterion (ΔAIC), an information-theoretic approach, was used to evaluate models for nest-site selection using the 11 variables described above (Burnham and Anderson 2001). We conducted three Akaike's information criterion corrected for small sample size (ΔAIC_c) analyses comparing the following: (1) successful ($n = 48$) to unsuccessful nests ($n = 14$), (2) nest sites ($n = 62$) to randomly selected mock nest sites off males' territories ($n = 186$), and (3) nest sites ($n = 62$) to randomly selected mock nest sites on males' territories ($n = 186$). The lowest ΔAIC_c value indicates the most parsimonious model; therefore, any of the vegetative components or combination of components within the model with the lowest value indicates the model that best balances goodness of fit to the data. Models that have a ΔAIC_c value ≤ 2.0 have substantial support. We do not discuss models > 2.0 because they have less support, but they are included in the tabulated results. Binary logistic regressions were calculated with SPSS version 14.0. We used $\alpha = 0.05$ and all results are stated as mean \pm SE.

Results

We found 62 nests over the 3 years of this study and 48 out of 62 were successful (77.4%). Nest success did not significantly differ among the years 2006 ($69.2\% \pm 0.13\%$), 2007 ($71.4\% \pm 0.12\%$), and 2008 ($89.1\% \pm 0.06\%$) ($F_{[2,54]} = 1.53$, $p = 0.226$). Of the 62 total nests, 42 were found north of the bog and 20 were found south of the bog. All nests for both plots for all 3 years were combined for analyses for reasons described in the Materials and methods.

The most parsimonious model predicting the structural habitat differences between successful nests ($n = 48$) and unsuccessful nests ($n = 14$) included higher densities of the smallest stems ($\Delta AIC_c = 0.00$; Table 1). A second model consisting of higher density of small stems and greater nest concealment was associated with nest success ($\Delta AIC_c = 0.60$; Table 1). Additional less parsimonious models included all higher densities of all three stem sizes ($\Delta AIC_c = 0.73$; Table 1), less amount of the nest visible (referred to hereafter as its converse), greater concealment ($\Delta AIC_c = 0.93$; Table 1), and greater amounts of coarse woody debris ($\Delta AIC_c = 1.31$; Table 1).

Concealment was significantly different when compared between actual nest sites and both types of mock nest sites ($F_{[2,420]} = 95.36$, $p < 0.0001$; Fig. 1). Post hoc tests revealed that nest sites had significantly more concealment ($86.69\% \pm 1.32\%$) than mock nest sites on territories ($50.58\% \pm 1.75\%$; $p < 0.001$) and off territories ($39.78\% \pm 1.92\%$; $p < 0.001$). Mock nest sites on and off territories were not significantly different from each other.

No solitary parameter significantly distinguished an actual nest site from a mock nest site off males' territories (Table 1). The model including higher numbers of the largest stems, greater amounts of coarse woody debris, and greater nest concealment was the most parsimonious in explaining the placement of a nest site ($n = 62$) when compared with non-territory mock nest sites ($n = 186$) ($\Delta AIC_c = 0.00$; Table 1). Three other parsimonious models include the following: (1) amount of small stems, nest concealment, number of ferns, and coarse woody debris ($\Delta AIC_c = 0.69$); (2) all three stem sizes, nest concealment, number of ferns, coarse woody debris, and moss ($\Delta AIC_c = 1.08$; Table 1); and (3) amount of largest stems, nest concealment, number of ferns, and coarse woody debris ($\Delta AIC_c = 1.12$; Table 1). In all three of these models, greater values were consistently associated with actual nest sites (greater concealment meaning lower percentage of nest visible).

In comparing on-territory mock nest sites to actual nest sites, no models with less than seven parameters explained any vegetation differences. The most parsimonious model included moss, ferns, leaf litter, coarse woody debris, concealment, small and medium-sized stems, and all tree stem sizes ($\Delta AIC_c = 0.00$; Table 1). Again, higher values for each variable were associated with actual nests.

Discussion

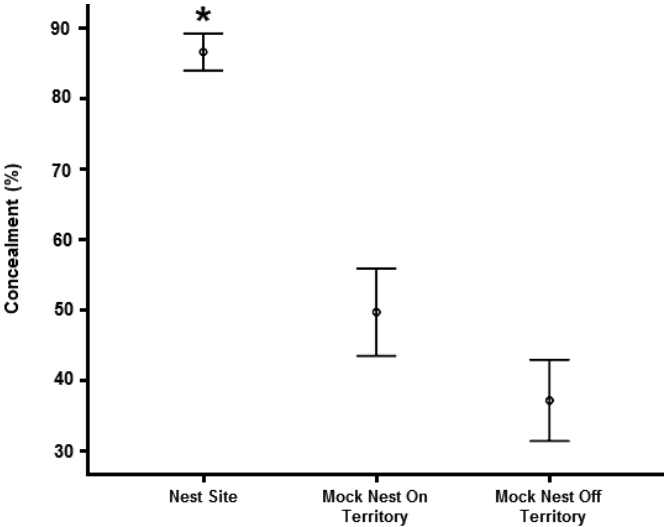
As we predicted, higher density of stems and greater nest concealment are nest-site features that both relate to success and distinguish the structure of territories of Canada Warblers from the surrounding forest. High stem density in particular is a characteristic identified to be important to this

Table 1. Results of AIC_c analyses explaining vegetative characteristics of nest sites of Canada Warblers (*Wilsonia canadensis*).

Model	AIC _c [*]	ΔAIC _c [†]
Successful nest sites vs. unsuccessful nest sites		
Smstem	66.13	0.00
Conceal + smstem	66.74	0.60
Allstem	66.86	0.73
Conceal	67.06	0.93
CWD	67.44	1.31
Fern	68.20	2.07
CWD + fern + smstem	69.92	3.79
Nest sites vs. mock nest sites off territories		
Conceal + CWD + lgstem	16.85	0.00
Conceal + CWD + fern + smstem	17.55	0.69
Allstem + conceal + CWD + fern + moss	17.92	1.08
Conceal + CWD + (sm + all) stems	17.97	1.12
Conceal + CWD + fern + lgstem	18.55	1.70
Conceal + CWD + fern + moss + smstem	19.62	2.77
Nest sites vs. mock nest sites on territories		
CWD + fern + LL + (sm + med + all) stems	46.72	0.00
Smstem	67.31	3.02
Conceal	118.12	4.24
Conceal + CWD + fern + moss + (sm + all) stems	145.12	4.60

Note: All model variables explained in methods.
^{*}Akaike's information criterion corrected for small sample size.
[†]Difference in Akaike's information criterion corrected for small sample size. conceal, concealment; CWD, coarse woody debris; LL, leaf litter; lgstem, large stem; medstem, medium-sized stem; smstem, small stem.

Fig. 1. Concealment (%; mean ± SE) of nest sites and randomly selected mock nest sites of Canada Warblers (*Wilsonia canadensis*) on and off territories. There was a significant difference in concealment between groups ($F_{[2,418]} = 95.36, p < 0.0001$; *, significant difference at $\alpha = 0.05$).



species when selecting habitat. Densities of smaller stems were particularly high immediately around nests when compared with either category of mock nests. Additional structural features of actual nest sites included high amounts of coarse woody debris, ferns, and moss as components of ground cover.

Canada Warblers select dense habitat structure at many different sites including our own (Robbins et al. 1989; Hallworth et al. 2008b; Chace et al. 2009). Bent (1953) also described nest sites of Canada Warblers as often being associated with coarse woody debris including stumps and downed logs. These features serve to increase ground substrate complexity and often create highly concealed nest sites and shelter from the weather (Götmark et al. 1995). In particular, many nests are built under the shelter of a fallen tree. Successful nests had higher densities of small woody stems and a greater amount of vegetative cover than failed nests. Rodewald and Yahner (2001) found a significantly greater number of trees and a marginally greater amount of nest concealment surrounding successful nest sites when compared with unsuccessful nest sites for ground nesters of numerous species in mature forest with patches of disturbance. Dense habitat structure and higher concealment are also potentially important to young fledglings, especially before they can fly well (King and DeGraaf 2006). No single variable distinguished actual nest sites from mock nests on territories, suggesting that habitat structure within territories could accommodate many nest sites. The actual location of nests may be influenced by additional factors such as distance to neighbors or availability of dense vegetation for newly fledged young. Importantly though, actual nest sites had a larger amount of vegetative cover compared with random mock nest sites on and off territories. In addition to the significance of vegetative cover, parental behaviors associated with concealing the nest are important adaptations particularly because the Canada Warbler has a

relatively short breeding season and a short window to attempt re-nesting if nests fail. Weidinger (2002) found artificial ground nests with good concealment to have fewer avian predation events but more rodent predation events when compared with nests in shrubs and trees. However, at active nests of Yellowhammers, a ground-nesting species, the presence of the adults significantly reduced the amount of rodent predation events. Female Canada Warblers have high nest attentiveness and do not readily flee from the nest until the threat is within 1 m (M.L. Goodnow and L.R. Reitsma, personal observation). The female also performs a fledgling decoy display when they do leave the nest to distract predators (Reitsma et al. 2010). Females' dull plumage (blue – slate gray) allow them to hide the location of the nest both with camouflage and by covering the movement of the nestlings that could potentially attract visual predators (Montgomerie and Weatherhead 1988; Martin 1992b). These data along with our observations suggest the importance in considering the affect of parental presence and associated predator avoidance behaviors along with the physical structure surrounding and concealing the nest.

Though many agree about the importance of parental behavior to reproductive success (e.g., Götmark et al. 1995; Weidinger 2002), several studies have not shown concealment to be a significant factor in affecting reproductive success (Martin 1992b; Burhans and Thompson 1998). For example, Howlett and Stutchbury (1996) measured concealment around the nest sites of Hooded Warblers (*Wilsonia citrina* (Boddaert, 1783)). They also experimentally removed vegetation from 15 nests and compared those with 15 control nests of the same breeding pair. In both instances, they found no effects of concealment on predation rates.

Hooded Warblers are shrub nesters that tend to have multiple broods (Chiver et al. 2011), whereas Canada Warblers are ground nesters with shorter breeding seasons that have not been documented double-brooding (Reitsma et al. 2010). Ground nesters have more need to conceal nests from a greater diversity of predators (avian, mammalian, and reptilian). Ground-dwelling predators have varying searching techniques and concealment is likely the best defense (Filiater et al. 1994). Concealment may not be the main predictor of potential success across all small passerine species, especially among non-ground-nesting species such as the Hooded Warbler. However, Canada Warblers benefit from having highly concealed nests and thus is a factor females potentially use in nest-site selection.

Female nest-site selection also likely influences male's selection of his territory as Steele (1993) found with Black-throated Blue Warblers (*Dendroica caerulescens* (Gmelin, 1789)). If a male's territory does not have nest sites considered adequate by the female, he would be less likely to successfully pair (Burke and Nol 1998). Ovenbirds (*Seiurus aurocapilla* (L., 1766)) paired and fledged young less successfully on territories with lower prey abundances and fewer potential nest sites (Burke and Nol 1998). Thus, male Canada Warblers may well consider the availability and number of suitable nest sites when establishing territories.

These results point to the value of conserving habitat with complex ground cover and high stem densities. Additionally, emergent trees above the understory are important as song perches (Hallworth et al. 2008a). This feature is not relevant

to nest-site selection, but may be important in attempts to colonize new areas. Ground cover that provides opportunities for highly concealed nests is critical to successful reproduction for this species in decline. Forests with disturbance regimes that can include partial harvesting with residual trees left standing and that feature moist forest floors with dense herbaceous and shrub layers are favored by this species. In contrast, mature, manicured, tidy forests are not selected by Canada Warblers. Conserving poorly drained forested lands (also referred to as forested wetlands) that are difficult to walk through and that have thick stems obscuring distant views will be increasingly important as humans encroach on such forest types traditionally regarded as wild and impenetrable.

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