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DO CROSS-SCALE CORRELATIONS CONFOUND ANALYSIS OF NEST SITE SELECTION FOR CHESTNUT-BACKED CHICKADEES?

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Abstract. Multiscale models of nest site selection often ignore cross-scale correlations (correlations between predictor variables at different scales). We reexamined nest site selection of Chestnut-backed Chickadees (*Poecile rufescens*) at two scales within territories to isolate: (1) variation associated purely with variables measured at the patch (0.031 ha) and tree scales, and (2) variation shared by variables measured at the patch and tree scales. We used conditional (fixed-effect) logistic regression to build a patch, tree, and full model, and subtracted pure and shared components of variation from the deviance explained by the full model. Tree scale and patch scale variables accounted for 85% and 9% of the total explained variation, respectively. Only 6% of explained variation in nest site locations was due to cross-scale correlations. We suggest that multiscale habitat selection studies incorporate a diagnostic tool like variance decomposition to avoid spurious results caused by lack of independence of habitat relationships.

Key words: *British Columbia, Chestnut-backed Chickadee, cross-scale correlations, habitat selection, multiscale model, nest site selection, variance decomposition.*

¿Confunden las Correlaciones entre Diferentes Escalas los Análisis de Selección del Lugar de Anidación en *Poecile rufescens*?

Resumen. Los modelos de escalas múltiples de selección del lugar de anidación usualmente no tienen en cuenta las correlaciones entre escalas (correlaciones entre variables predictivas a diferentes escalas). Reexaminamos la selección del lugar de anidación en *Poecile rufescens* a dos escalas en los territorios con el fin de aislar: (1) la variación pura asociada con las variables medidas a las escalas de parche (0.031 ha) y de árbol, y (2) la variación compartida por variables medidas a las escalas de parche y de árbol. Usamos regresiones logísticas condicionales (efecto fijo) para construir un modelo de parche, árbol y completo, y substrajimos los componentes puros y compartidos de la variación del desvío explicado por el modelo completo. Las variables a escala de árbol y de parche explicaron el 85% y el 9% de la variación total explicada, respectivamente. Sólo el 6% de la variación explicada en la localización del lugar de anidación se debió a las correlaciones entre escalas diferentes. Sugerimos que los estudios de selección de hábitat a múltiples escalas incorporen una herramienta de diagnóstico como la descomposición de la varianza, para evitar resultados espurios causados por la falta de independencia de las relaciones de hábitat.

Examining patterns of habitat selection is often a key component of any study exploring bird-habitat relationships. Habitat selection is thought to be a hierarchical process, with selection occurring at multiple spatial scales (Johnson 1980, Jones 2001, Manly et al. 2002, Kristan 2006). Studies of nest site selection compare habitat variables at used sites (e.g., a nest tree) and unused sites (e.g., a tree not used for nesting) and assess whether differential resource selection occurs (i.e., disproportionate use of habitat variables). Comparisons can be made across multiple spatial scales, with many studies examining patterns of resource selection at three scales: home range or territory (e.g., habitat size, composition, location, and configuration), patch or local (e.g., microhabitat structure and composition), and tree (e.g., tree height, size, decay stage).

Despite designing nest site selection studies to look for evidence of habitat selection at multiple spatial scales, most researchers analyze associations at each scale separately. Although this type of analysis can provide information about habitat selection at each scale, it ignores relationships among scales that occur due to cross-scale correlations (correlations between predictor variables at different scales). For example, large trees in old stands often have clumped spatial distributions, resulting in a cross-scale correlation between the fine-scale variable for tree size and the coarse-scale variable of stand age (Battin and Lawler 2006). Cross-scale correlations among variables lead to difficulties in interpreting results; particularly, difficulties in determining which variables and which scales are driving the observed pattern (Cushman and McGarigal 2002, Battin and Lawler

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2006). When strong correlations exist across variables (i.e., multicollinearity) at different scales, habitat relationships identified at any scale may not be independent of other scales (Lawler and Edwards 2006). Given the importance of nest site selection studies for identifying suitable breeding habitat for species classified as endangered, threatened, rare, or of special management concern, gaining a better understanding of the appropriate scale or scales at which to manage habitat is critical.

Our previous examination of Chestnut-backed Chickadee (*Poecile rufescens*) nest site selection at separate scales (Mahon et al. 2007) raised three questions: how important are variable groups at each scale, what is the nature of cross-correlations among scales, and which habitat scale influences the process of nest site selection? In our system, the ecological processes (disease outbreaks, insect activity, and wind storms) that create important nest tree attributes for Chestnut-backed Chickadees often occur in groups or patches within stands. Diseased trees tend to appear in clusters within stands, since diseases such as *Armallaria* root rot are transferred to neighboring trees through direct contact or dispersion of spores. As another example, trees with broken tops (broken-top trees) resulting from wind damage are often spatially clustered because wind effects can be greater along an exposed edge or along a steep cliff. As a result, measures at the nest patch and nest tree scales are likely correlated. We questioned whether these correlations among variables at the two spatial scales were strong enough to influence patterns of nest site selection (i.e., whether selection at the tree scale was influenced by selection at the patch scale).

Partitioning variation into additive effects can be used to assess the impacts of variables, or sets of variables, where there is evidence of multicollinearity. For linear models fitted using least squared error as the objective, the residual sums of squares can be partitioned (Whittaker 1984, Kutner et al. 2005). This can also be represented as partial coefficients of determination for each variable or for groups of variables. For models fitted using maximum likelihood as the objective, the deviance can be partitioned (Whittaker 1984). Using these approaches, the variation in the response variable can be partitioned into variation uniquely attributable to each variable ("primary elements"; Whittaker 1984), versus variation that can be ascribed to any of the variables ("secondary elements" and "higher level elements"; Whittaker 1984). In a multiscale model, Lawler and Edwards (2006) used the approach developed by Whittaker (1984) to partition the variation by groups of variables, where each group was measured at a particular scale. They termed the primary elements "pure components," whereas the secondary and higher elements were termed "shared components." The advantages to using this variation partitioning approach are that: (1) the variation that is strictly due to each set of variables at a particular scale can be determined; (2) the overlap in contributions can be determined; and (3) any overlap in contribution can be interpreted as being competitive (response of variables is opposite or negative) or complementary (response of variables is similar or positive; Whittaker 1984).

Using the "decomposition of variation" approach described by Whittaker (1984) and used by Lawler and Edwards (2006), we reexamined patterns of nest site selection of a weak cavity excavator, the Chestnut-backed Chickadee, across a range of uncut and partially cut stands in northwest British Columbia. Our objectives were to: (1) assess selection of nesting habitat by Chestnut-backed Chickadees at two spatial scales located within territories—the patch scale (0.031 ha plot), and the tree scale, (2) isolate the variation in nest site locations uniquely attributable to the variables measured at the patch scale and at the tree scale, and (3) isolate the variation in nest site locations that was shared by a combination of variables measured at the patch and tree scales. This analysis allowed us to assess the strength of the effects of variables at each scale and interpret any cross-scale correlations relative to nest site selection patterns at each scale.

METHODS

STUDY AREA

The McCully Creek watershed (55°22′N, 127°50′W) is located in northwest British Columbia, Canada, approximately 35 km north of the town of Hazelton in the Interior Cedar-Hemlock moist cold (ICHmc) biogeoclimatic subzone (150–1000 m elevation), within the coast–interior transition area (Banner et al. 1993). Mature forest stands (140 years old) within this temperate, humid environment were dominated by western hemlock (*Tsuga heterophylla*), but also included western redcedar (*Thuja plicata*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), hybrid spruce (the complex of white spruce [*Picea glauca*], Sitka spruce [*P. sitchensis*], and Engelmann spruce [*P. engelmannii*]), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and black cottonwood (*P. balsamifera*). Amabilis fir (*Abies amalilis*) also occurred at higher elevations. Old-growth forests (250–300+ years old) were dominated by western hemlock, with major components of subalpine and amabilis fir, and western redcedar. Zonal ecosystems consisted of a thick moss layer dominated by feather mosses and a poorly developed herb and shrub layer (Coates et al. 1997). Natural disturbance patterns in the ICHmc are characterized by frequent small-scale, low-intensity, gap-forming disturbances operating at the individual tree scale (Coates and Burton 1997). Treefall gaps of various sizes are created by natural tree mortality, wind, fungi, and insect activity (Banner et al. 1993). Important diseases include heart rots like red ring rot (*Phellinus pini*), red belt fungus (*Fomitopsis pinicola*), and Indian paint fungus (*Echinodontium tinctorium*), and root rots like tomentosus root rot (*Inonotus tomentosus*) and Schweinitzii butt rot (*Phaeolus schweinitzii*), while insects include the mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*D. rufipennis*), western balsam bark beetle (*Dryocoetes confusus*), western hemlock looper (*Lambdina fiscellaria lugubrosa*), and two-year-cycle budworm (*Choristoneura biennis*).

We monitored three uncut sites and five partially cut sites ranging from low intensity (30% of the stand volume removed as single trees and small patch cuts) to high intensity harvest (60% of the stand volume removed with 30% in openings of 0.1–0.5 ha and 30% as single trees between openings; Coates et al. 1997). Study sites (19–24 ha) represented a gradient of stand conditions, containing small and large treefall gaps surrounded by a matrix of uncut and thinned forest (single tree removal). Sites were within mature (145 years old) and old-growth (353–373 years old) forest stands at elevations ranging from 455 to 665 m. All study sites were not spatially separated or isolated and therefore were not completely independent of one another. Additional details of study sites are given by Mahon (2006) and Mahon et al. (2007).

DATA COLLECTION

We monitored Chestnut-backed Chickadee pairs in six sites in 2000 (preliminary year) and eight sites from 2001 to 2003 using line transect surveys (Bibby et al. 2000) and behavioral observations.

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We established a 50 m grid system in each site. Three times per week between early May and mid-June we surveyed every second grid line along one bearing and recorded all birds heard or seen. We then followed all chickadee pairs or individuals (pairs were monomorphic) detected during the survey and recorded location, number of individuals, and behavior on 1:4000 scale site maps referenced to the 50 m grids. We recorded locations at 5 min intervals (Hill and Lein 1989) to determine territory boundaries and searched areas where birds were observed exhibiting breeding behaviors to locate active nests (Martin and Geupel 1993). Chestnut-backed Chickadees are weak cavity excavators that use a variety of nest sites in mature and old conifer-dominated forests: branch holes, cracks, wound sites, and broken tops. This species also uses secondary cavities, which are excavated by other weak cavity excavators (nuthatches, chickadees) or strong cavity excavators (woodpeckers) but then renovated by chickadees.

We assessed vegetation characteristics within circular plots of 10 m radius (0.031 ha) centered at all active nest trees (nest plot) and at a close plot (centered on the nearest grid point location to the active nest located within the chickadee territory). Here, we limit our description of habitat to those variables previously identified as biologically relevant to Chestnut-backed Chickadee nest site selection (Table 1; Mahon et al. 2007).

Within all plots we visually estimated percent canopy cover (ocular estimate to the nearest 5%) of trees >12.5 cm in diameter. For each tree (>12.5 cm diameter) within all plots we recorded tree species, dbh (diameter at breast height taken 1.3 m above ground), whether the tree was live or dead, and tree health using standardized tree mensuration procedures for collecting ecological data in British Columbia (British Columbia Ministry of Forests 1998). A tree was classified as diseased or attacked if we detected the presence of any disease (stem, root, or butt rot, trunk gall, mistletoe) or insect activity. We recorded the presence of three specific damage agents: conks (fungal fruiting bodies), boring insects (exit holes, galleries, pitch tubes), and broken tops.

For all plots, we summarized the density of vegetation per 0.031 ha sampling plot (percent canopy cover, density of trees, density of diseased or attacked trees, and density of broken-top trees). Vegetation characteristics (Table 1) were measured in nest and close plots from 2000 to 2003. Using this sampling scheme, we compared used versus unused habitat at two scales within the territory of each Chestnut-backed Chickadee pair. At the patch scale, we compared nest plots to close plots within the territory of the nesting chickadee pair. At the tree scale, we compared nest trees to non-nest trees within close plots. We did not assume a constrained study design in which the bird first selects a home range or territory, then a nest patch, and then a nest tree within the nest patch. Our sampling design was constrained only at the territory scale (i.e., the territory constrained the nest patch and nest tree location), because it is unclear whether Chestnut-backed Chickadees select nesting habitat using a top-down approach (i.e., choose coarse-scaled habitat features first) or a bottom-up approach (i.e., choose fine-scaled habitat features first; Kristan 2006).

TABLE 1. Descriptions of variables measured to assess nest site selection patterns of Chestnut-backed Chickadees at two spatial scales at McCully Creek, British Columbia, 2000–2003.

Variable	Description
Patch variables[a]	
CanCov	Percent canopy cover (trees >10 m tall)
DensTrees	Number of trees >12 cm diameter at breast height (dbh)
DensDead	Number of snags >12 cm dbh
DensDis	Number of diseased trees >12 cm dbh
DensBT	Number of trees with broken tops >12 cm dbh
Tree variables	
DBH	Diameter of tree at breast height
Live	Condition of tree (live or dead)
BT	Presence of broken top
CO	Presence of fungal conks
BI	Presence of boring insects

[a]All patch scale variables represent the density of vegetation (percent cover, density of trees) per 0.031 ha sampling plot.

STATISTICAL ANALYSES

We used the "decomposition of variation" approach described by Whittaker (1984) and Lawler and Edwards (2006) to quantify the variation in Chestnut-backed Chickadee nest locations associated with habitat variables we previously identified as important at the patch and tree scales (Mahon et al. 2007). We first fit a conditional (fixed-effects) logistic model for each spatial scale. We used our a priori knowledge of nest site selection patterns of Chestnut-backed Chickadees (Mahon and Martin 2006, Mahon et al. 2007) to select biologically relevant variables at each scale. We limited the number of variables included in our models due to our small sample size of nests ($n = 61$). We developed candidate sets of models at each scale (patch = 25 models; Appendix A; tree = 25 models; Appendix B) using all possible combinations of variables and used Akaike's information criterion corrected for small sample size (AIC_c), ΔAIC_c, Akaike weights (w_i), and weighted averages to select the best model at each scale (Burnham and Anderson 1998). We then used all of the variables included in the best patch and tree models to build a full model with variables measured at both scales. For all models, we used deviance expressed as a percentage of the null (intercept only) model (percent deviance) using McFadden's R^2 or McFadden's likelihood ratio index (logistic extension of the percent variance explained; Hardin and Hilbe 2001). Variations attributable to patch level and tree level variables were calculated as follows:

$$\text{Pure patch percent deviance} = \text{percent deviance (Full Model)} - \text{percent deviance (Tree)},$$

$$\text{Pure tree percent deviance} = \text{percent deviance (Full Model)} - \text{percent deviance (Patch)}.$$

The shared variation was then calculated as:

$$\text{Shared percent deviance} = \text{percent deviance (Full Model)} - \text{percent deviance (Pure Patch)} - \text{percent deviance (Pure Tree)}.$$

The percentages of variation explained by each additive term, relative to percent deviance for the full model, were also calculated. All analyses were performed using STATA version 9.0 (StataCorp 2005).

RESULTS

We located 69 Chestnut-backed Chickadee nests in 61 natural cavities within our study sites in the McCully Creek study area (Mahon et al. 2007). At the patch scale, chickadee nests were located in patches with high densities of broken-top trees. At the tree scale, nests were located in large trees with broken tops,

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TABLE 2. Composition and fit of three conditional (fixed-effect) logistic regression models for assessing Chestnut-backed Chickadee nest site selection. The models were used to partition the variance in nest use associated with habitat factors at two spatial scales (patch = 0.031 ha, and tree). See Table 1 for explanations of model variables.

Model	Variables	Percent deviance explained
Full	DensBT + DBH + BT + CO + BI	R^2 MF[a] = 40
Patch	DensBT	R^2 MF = 6
Tree	DBH + BT + CO + BI	R^2 MF = 37

[a] R^2 MF is McFadden's likelihood ratio index (logistic extension of the percent variance explained).

conks, and boring insects. The full model, including variables from both the patch scale and the tree scale, explained 40% of the variation in nest site locations (Table 2).

The isolated components of variation used to assess the relative importance of factors at each of the two spatial scales showed that the largest component of variation was attributable to tree scale variables (tree size and whether the tree had a broken top, fungal conks, and boring insects), with 85% of the total explained variation (Table 3). In comparison, patch scale variables accounted for only 9% of the total explained deviance and only 6% of the explained variation in nest site locations was attributed to cross-scale correlations.

DISCUSSION

We found that about 85% of the explained deviance in models of Chestnut-backed Chickadee nest site selection could be attributed to variables measured at one spatial scale—the tree scale. Understanding how birds select habitat may provide some answers as to why nest tree variables explained the highest amount of variation in our data and why there was so little evidence of cross-scale correlations between patch- and tree-scale variables. Habitats often have a hierarchical structure in which some variables are components of other variables (Kristan and Scott 2006). In addition, how birds respond to habitats at different scales can form an information hierarchy within which birds consider multiple scales of information when selecting a habitat (Kristan 2006). For example, a forest-dwelling passerine may choose a stand based on the composition, structure, and age of the stand. When selecting an area within the stand to locate a breeding territory, birds will consider multiple scales of information: canopy, subcanopy, and understory composition and structure required for foraging and protective cover, but also specific structural attributes (e.g., trees, snags, shrub patches, coarse woody debris, and upturned tree roots) required for nesting. If birds select habitat sequentially (at different scales or levels of a hierarchy), then information correlated across spatial scales can be considered part of the habitat scale that the bird selects first. Our understanding of the importance of a scale then depends on which scale we assume the bird selects first (Kristan 2006). Birds can select habitat by selecting fine-scaled features first (e.g., nest tree, where the correlation between fine- and coarse-scaled features is entirely an effect of the fine-scaled features) or coarse-scaled features first (e.g., forest type, where the correlation between fine- and coarse-scaled features is entirely an effect of the coarse-scaled feature).

TABLE 3. Variation in nest site locations of Chestnut-backed Chickadees explained by habitat factors at two spatial scales. Pure components of variation are those that can be attributed to variables at one scale. Shared components of variation are those that cannot be attributed to factors at any one scale, due in part to cross-scale correlations.

Additive components of variation	Percent deviance explained	Percent of total deviance explained
Pure (Patch)	3.6 (= 40.4 – 36.8)	100 × (3.6/40.4) = 9%
Pure (Tree)	34.2 (= 40.4 – 6.2)	100 × (34.2/40.4) = 85%
Shared (Patch + Tree)	2.6 (= 40.4 – 3.6 – 34.2)	100 × (2.6/40.4) = 6%

Weak cavity excavators require nest trees with specific attributes (Ficken et al. 1996, Ghalambor and Martin 1999, Dahlsten et al. 2002, Martin et al. 2004). For Chestnut-backed Chickadees, these attributes include an entry point (wound site, broken top, broken branches, or crack) and a diseased area that allows excavation of soft heartwood (Dahlsten et al. 2002, Mahon et al. 2007). If Chestnut-backed Chickadees first select a suitable nest tree, then any patch-scale features would be an effect of the chosen nest tree. This could explain the large component of variation at the tree scale (85%) and the relatively small component of variation at the patch scale (9%).

Our results showed that the shared component of variation was positive and therefore complementary, rather than competitive (terminology by Whittaker 1984), indicating that there was a positive relationship between tree and patch scales of measurement. However, since the amount of variation explained was only 6%, the cross-scale correlations were not strong for the two scales we examined. In our system, chickadees exhibited strong selection for suitable nest trees, but appeared to select diverse nest patches that allowed them to meet a variety of other habitat requirements (foraging, perching, and parental care). For example, during the nestling stage, both adults made many foraging trips to the nest; a productive nest patch enabled one or both parents to forage near the nest, increasing both foraging efficiency (i.e., reducing the distance and time to capture prey items) and vigilance. Productive foraging habitat for Chestnut-backed Chickadees could be found throughout the stand in a variety of habitat types; chickadees foraged in mature conifer and deciduous trees within the closed canopy of the forest matrix and in young conifers and saplings found in natural and harvested openings (Mahon 2006).

Our results differ from those of Lawler and Edwards (2006), who examined the influence of cross-scale correlations for the Red-naped Sapsucker (*Sphyrapicus nuchalis*) and Northern Flicker (*Colaptes auratus*) at the home range, local, and tree scales. They found a similar contribution from pure and shared components, with almost half of the explained deviance attributed to shared explanatory factors from multiple cross-scale combinations. Shared associations across scales explained a large percentage of the deviance in the local and home range scale models (compared to the tree scale model), suggesting stronger associations among habitat variables at these two larger scales. Our low shared component of variation could have resulted from examining habitat associations at relatively small scales (i.e., tree and patch), instead of all spatial scales associated with breeding season habitat selection (i.e., tree, patch, and home range).

Studies of multiscale habitat selection should determine if cross-scale correlations among variables exist. Failure to detect

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these relationships can lead to spurious results caused by lack of independence of habitat relationships and uncertainty about which variables and which scales drive patterns of habitat selection. We suggest that all multiscale habitat selection studies incorporate a simple diagnostic tool such as variance decomposition to detect the presence and strength of cross-scale correlations. In addition, we recommend examining all relevant habitat scales to determine which variables and which scales strongly influence the process of selection. For example, the Pileated Woodpecker (*Dryocopus pileatus*) selects large trees for nesting and roosting (mean dbh >55–97 cm in a variety of habitats) and old stands with large live and dead trees and downed logs (containing ants and beetles) for foraging (Bull and Jackson 1995), suggesting a correlation between variables at fine scales (e.g., tree) and those at coarse scales (e.g., stand type). Although many studies now examine habitat features and species responses at several biologically relevant scales (i.e., scales relevant to how animals perceive and respond to habitat), researchers also need to consider how variables at multiple scales might be related

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APPENDIX A. Patch scale conditional (fixed-effect) logistic regression models to predict nest site use by Chestnut-backed Chickadees at McCully Creek, British Columbia, 2000–2003. Models are ranked from best to worst based on the difference from the top model in Akaike's information criterion corrected for small sample size (ΔAIC_c). K is the number of parameters in the model, $-2(L)$ is -2 times the log-likelihood, and w_i is an estimate of the likelihood of the model given the data; normalized to sum to 1. See Table 1 for explanations of model variables.

Patch scale model	$-2(L)$	K	ΔAIC_c [a]	w_i
DensBT	79.36	2	0.00	0.243
DensDead + DensBT	79.01	3	1.75	0.101
CanCov + DensBT	79.01	3	1.75	0.101
DensTrees + DensBT	79.29	3	2.03	0.088
DensDis + DensBT	79.34	3	2.08	0.086
CanCov + DensDis + DensBT	78.67	4	3.55	0.041
DensTrees + DensDis + DensBT	78.67	4	3.55	0.041
DensDead + DensDis + DensBT	78.93	4	3.81	0.036
DensDead	83.24	2	3.88	0.035
CanCov	83.37	2	4.01	0.033
DensTrees	83.65	2	4.29	0.028
DensTrees + DensDead + DensDis + DensBT	77.49	5	4.54	0.025
DensDis	83.94	2	4.57	0.025
CanCov + DensDead + DensDis + DensBT	78.25	5	5.31	0.017
CanCov + DensDead	82.78	3	5.52	0.015
DensTrees + DensDead	83.19	3	5.93	0.012
DensDead + DensDis	83.24	3	5.98	0.012
CanCov + DensTrees	83.28	3	6.02	0.012
CanCov + DensDis	83.33	3	6.07	0.012
DensTrees + DensDis	83.64	3	6.38	0.010
CanCov + DensTrees + DensDead + DensDis + DensBT	77.38	6	6.65	0.009
CanCov + DensDead + DensDis	82.66	4	7.54	0.006
CanCov + DensTrees + DensDead	82.73	4	7.61	0.005
DensTrees + DensDead + DensDis	83.12	4	8.00	0.004
CanCov + DensTrees + DensDead + DensDis	82.66	5	9.71	0.002

[a]The AIC_c value for the top model (DensBT) was 83.46 (n = 122 nest and close plots).

APPENDIX B. Tree scale conditional (fixed-effect) logistic regression models to predict nest site use by Chestnut-backed Chickadees at McCully Creek, British Columbia, 2000–2003. Models are ranked from best to worst based on the difference from the top model in Akaike's information criterion corrected for small sample size (ΔAIC_c). K is the number of parameters in the model, $-2(L)$ is -2 times the log-likelihood, and w_i is an estimate of the likelihood of the model given the data; normalized to sum to 1. See Table 1 for explanations of model variables.

Tree scale model	$-2(L)$	K	ΔAIC_c [a]	w_i
DBH + BT + CO + BI	229.51	5	0.00	0.655
DBH + Live + BT + CO + BI	229.24	6	1.75	0.274
DBH + BT + CO	237.02	4	5.49	0.042
DBH + Live + BT + CO	236.00	5	6.49	0.026
DBH + BT	245.61	3	12.08	0.002
DBH + Live + BT	243.89	4	12.36	0.001
BT + CO + BI	246.99	4	15.47	0.000
Live + BT + CO + BI	246.62	5	17.11	0.000
BT + CO	256.74	3	23.20	0.000
BT + BI	257.07	3	23.54	0.000
Live + BT + CO	256.74	4	25.21	0.000
BT	269.67	2	34.12	0.000
Live + BT	269.51	3	35.97	0.000
DBH + Live	278.44	3	44.90	0.000
Live + CO + BI	283.75	4	52.23	0.000
DBH + CO + BI	287.75	4	56.23	0.000
Live + CO	296.32	3	62.78	0.000
Live + BI	298.93	3	65.39	0.000
CO + BI	301.27	3	67.73	0.000
DBH + BI	309.81	3	76.27	0.000
Live	313.02	2	77.47	0.000
DBH + CO	316.16	3	82.62	0.000
BI	325.11	2	89.57	0.000
CO	331.89	2	96.34	0.000
DBH	343.75	2	108.21	0.000

[a]The AIC_c for the top model (DBH + BT + CO + BI) was 239.56 (n = 1386 nest and unused trees).

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