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Role of topography, canopy structure, and floristics in nest-site selection and nesting success of canopy songbirds

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ABSTRACT

Although oaks (*Quercus* spp.) have historically dominated many forests in eastern North America, forest composition is changing due to anthropogenic impacts on disturbance regimes. Silvicultural practices, such as partial harvesting, are one component of management to promote oak regeneration. From 2007 to 2009 our research examined nest-site selection and nesting success for a guild of five canopy songbirds in upland mixed-oak forests in southeastern Ohio, USA. We monitored >700 nests across three state forests in both open canopy shelterwood stands harvested to approximately 50% stocking, and closed-canopy mature second-growth. Habitat attributes, including topography, canopy structure, and floristics, were measured at nest sites and random plots $\leqslant$100 m from nests representing microhabitat available within the territory. Canopy songbirds selected specific topographic microclimates: Eastern Wood-pewees (*Contopus virens*) nested on xeric ridgetops, Blue-gray Gnatcachers (*Polioptila caerulea*) favored valleys, and Cerulean Warblers (*Dendroica cerulea*) preferred productive northeast-facing slopes. Nest sites differed among species in terms of concealment, nest support, topographic position on the slope, and basal area of trees >38 cm dbh. Four of the five focal species selected *Quercus alba* as the nest substrate more than twice as much as available, and three species avoided *Quercus rubra*. Daily survival rates of nests were negatively associated with basal area of red oak species (both *Quercus velutina* and *Q. rubra*) for several species individually and across the canopy-nesting guild. Additional factors related to success included time of season for Eastern Wood-pewees, nest age for Cerulean Warblers, and concealment and size of the support branch for Scarlet Tanagers (*Piranga olivacea*). In the long-term management for oak regeneration could benefit canopy songbirds, but our results indicate that white oaks, especially *Q. alba*, may be preferable to red oak species.

1. Introduction

Restoring the structure and function of pre-European settlement forest conditions is an important component of ecosystem management, which seeks to maintain the integrity of forests (Christensen et al., 1996; Grumbine, 1994). Although disturbance regimes that maintain forest ecosystems are not completely understood, poor oak (*Quercus* spp.) regeneration in the central hardwoods of North America suggests closed canopy second-growth stands of today may not be representative of historic conditions (e.g. Lorimer, 1984; Nowacki and Abrams, 2008). Dominant for the past 10,000 years (Davis, 1983), oaks are a disturbance-dependent climax community thought to be maintained by regular low-intensity wildfires (overview in Abrams (1992)). Growth rings show canopy disturbance may have competitively released trees every 20–30 years prior to European settlement (Abrams et al., 1995). Consistent with this, early explorers to the region often described open park-like woodland (e.g. Bartram, 1791; Denevan, 1992).

Oaks have high ecological, as well as commercial, value (McShea and Healy, 2002). Forest management practices that emulate historic disturbance regimes to promote oak regeneration are becoming widespread (Yaussy et al., 2008). Shelterwood harvesting, generally followed by prescribed fire, is one management technique used to open the canopy, and benefit shade intolerant oaks (Brose and Van Lear, 1998; Brose et al., 1999a,b; Loftis, 1990). However, current oak management recommendations are for stand replacement and even-aged regeneration. To be effective in the long term, restoration of forest ecosystems to historic conditions requires a more complete understanding of specific habitat requirements for plant and animal species.

Canopy-nesting songbirds are often associated with canopy disturbance, although reasons for these associations remain unclear (Ellison, 1992; Hamel, 2000; McCarty, 1996; Mowbray, 1999; Rodewald and James, 1996). Populations of one canopy species, the Cerulean Warbler, have experienced the largest decline of

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Table 1
Means and standard errors of basal area ($m^2\ ha^{-1}$) by tree size and tree species groups in recent shelterwood harvests with approximately 50% stocking (1–3 years post-harvesting) and unharvested upland mixed-oak forest (80–130 years) in southeastern Ohio, 2007–2009.

Location latitude/longitude	Site	Harvest?	Total basal area	Trees > 38 cm dbh	Trees 23–38 cm dbh	Xerophytic oak spp.[a]	Mesophytic tree spp.[b]	White oak spp.[c]	Red oak spp.[d]	*n*
Zaleski State Forest	KH	No	21.6 (1.1)	13.4 (1.0)	5.2 (1.0)	7.4 (1.1)	3.0 (0.7)	7.4 (1.1)	7.4 (1.2)	26
82° 18′/39° 19′	LR	No	24.5 (1.3)	14.5 (1.3)	6.1 (0.8)	7.5 (1.3)	5.5 (1.1)	6.2 (1.0)	7.0 (1.3)	25
	SS	Yes	9.8 (0.6)	7.7 (0.6)	2.0 (0.4)	4.9 (0.6)	0.5 (0.4)	4.7 (0.5)	4.1 (0.6)	38
	MH	Yes	13.3 (1.2)	7.5 (0.9)	5.5 (1.1)	4.0 (0.9)	1.5 (0.6)	6.4 (1.0)	4.2 (1.0)	23
Vinton Furnace Experimental Forest	R2	No	24.6 (0.8)	13.6 (0.8)	6.9 (0.6)	5.2 (0.7)	3.9 (0.6)	8.7 (0.7)	5.7 (0.7)	61
82° 22′/39° 11′	R3	No	23.8 (1.1)	14.5 (0.9)	6.9 (0.7)	3.7 (0.7)	6.0 (1.1)	6.8 (0.9)	4.3 (0.7)	47
	R1	No	22.3 (1.3)	9.5 (1.1)	8.6 (1.0)	3.5 (0.8)	1.6 (0.4)	10.1 (1.4)	3.4 (0.6)	43
	AR	No	23.9 (1.1)	12.6 (0.9)	7.9 (1.2)	11.8 (1.5)	1.4 (0.5)	13.7 (1.5)	4.3 (1.0)	23
	R3	Yes	12.3 (0.8)	7.6 (0.8)	4.1 (0.7)	2.7 (0.8)	1.9 (0.6)	2.1 (0.6)	5.7 (1.0)	23
	R1	Yes	17.4 (1.3)	6.2 (1.0)	7.7 (0.9)	4.4 (1.0)	0.3 (0.2)	7.7 (1.2)	5.0 (0.8)	22
	WO	Yes	9.5 (0.7)	8.5 (0.7)	1.0 (0.3)	3.2 (0.6)	0.0 (0.0)	4.6 (1.5)	4.3 (0.7)	25
Richland Furnace State Forest	GS	No	24.5 (1.2)	9.7 (1.0)	10.6 (1.1)	6.0 (1.8)	6.2 (1.2)	8.8 (1.4)	3.9 (0.9)	25
82° 36′/39° 10′	ON	No	23.4 (1.3)	12.0 (0.9)	8.0 (1.0)	7.8 (1.7)	2.8 (0.8)	12.9 (1.5)	1.9 (0.6)	24
	FP	Yes	9.6 (0.8)	7.3 (0.8)	2.0 (0.5)	5.2 (0.7)	0.5 (0.3)	4.2 (1.0)	4.0 (0.7)	30
	WS	Yes	11.5 (0.6)	9.5 (0.6)	1.9 (0.6)	4.4 (0.8)	0.2 (0.2)	6.1 (0.6)	4.0 (0.5)	29

[a] Xerophytic oak spp.: *Q. montana*, *Q. velutina*, and *Q. coccinea*.

[b] Mesophytic tree spp.: *L. tulipfera*, *A. saccharum*, and *F. grandifolia*.

[c] White oaks spp.: *Q. alba* and *Q. montana*.

[d] Red oaks spp.: *Q. rubra*, *Q. velutina*, and *Q. coccinea*.

any eastern forest bird (Link and Sauer, 2002; Sauer et al., 2008). Our study aimed to identify important habitat features for canopy songbirds, such as the declining Cerulean Warbler. Nest-sites are a critical component of fitness (review in Lima, 2009; Martin, 1998), and we developed models to examine the role of topography and microhabitat in nest-site selection and nesting success of individual canopy species and the canopy-nesting guild.

2. Methods

2.1. Study system

Research was conducted in southeastern Ohio in Vinton and Jackson Counties from 2007 to 2009. Study sites were located in three state forests separated by 15–30 km: Zaleski (ZSF), Vinton Furnace Experimental Forest (VFEF; formerly Raccoon Ecological Management Area), and Richland Furnace (RFSF) (Table 1). Study areas were predominantly forested (75–83% forest in a 10 km radius), and elevation ranged from 240 to 340 m. Newell and Rodewald (in press) provide a more complete description. Four sites (12–20 ha each) were located within a 1–3 km radius in each forest with additional areas at VFEF as part of the Cooperative Cerulean Warbler Forest Management Project (CCWFMP). Stands were characterized by 80–130 year old upland mixed-oak forest (Table 1, Fig. 1). Partial harvesting occurred at half of the sites in each forest from 2005 to 2006, generally reducing the stand to approximately 50% stocking (unharvested: 23.6 $m^2\ ha^{-1}$, 92% canopy closure; partial harvest: 11.5 $m^2\ ha^{-1}$, 50% canopy closure). Harvest areas ranged in size from 10 to 30 ha with oaks preferentially retained as residual trees as part of management for oak regeneration. In mature forest replacement of oaks by maples was apparent in the small tree size classes (Newell, 2010). Study sites were marked with grid flags at 50-m intervals for orientation.

2.2. Study species

We focused on a guild of five canopy songbirds that typically breed in southeastern Ohio: Eastern Wood-pewee (*Contopus virens*), Yellow-throated Vireo (*Vireo flavifrons*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Cerulean Warbler (*Dendroica cerulea*), and Scarlet Tanager (*Piranga olivacea*). These species all nest in the forest canopy but belong to different families (Tyrannidae, Vireonidae, Sylviidae, Parulidae, Cardinalidae). Species were selected based on previous experience of their presence and nesting behavior in the area. American Redstart (*Setophaga ruticilla*) was the only other possible candidate breeding in the area but generally nests and forages lower (George, 2009; Sherry and Holmes, 1997).

2.3. Nest monitoring

Nest searching and monitoring were conducted at all sites from 2007 to 2008; in 2009 half of the sites were studied. Territories were identified during settlement, and we focused on finding the first nesting attempts while birds were building. Later in the season we searched for renests in the territory within a few days after a nest failed. Two-thirds of nests were found during building. We searched for and monitored nests from the earliest Blue-gray Gnatcatchers building at the end of April until the last Eastern Wood-pewee nests fledged around the end August; in 2009 field work was finished at the end of July. Nests were checked every 2–3 days until failure or fledging. If there was no activity, we watched for 20 min (or 40 min if the female could not be seen on the nest) and checked again subsequently. A nest was considered to have failed if it was inactive prior to the earliest possible fledging date, estimated from known initiation dates for nests found during building. For nests found later in the nesting cycle, we used additional behavioral observations, including absence of active provisioning and immediate renesting without any sign of young. Provisioning observations for 30 min were used to help age young; behavior such as begging calls and active fully feathered chicks indicated young were close to fledging. We used the last active date for nests with uncertain fate (Manolis et al., 2000). Four nests that fledged only a brood parasite, the Brown-headed Cowbird (*Molothrus ater*), were considered to be nest failures.

2.4. Measurements of habitat characteristics

Habitat data were collected in July and August at random and nest plots each year. Nest plots were centered under the nest and random plots were placed using a stratified-random approach: one grid flag was selected per hectare, and the plot was placed a random direction and distance $\leqslant$50 m from the grid flag. Data at random plots were collected at all sites from 2007 to 2008; in

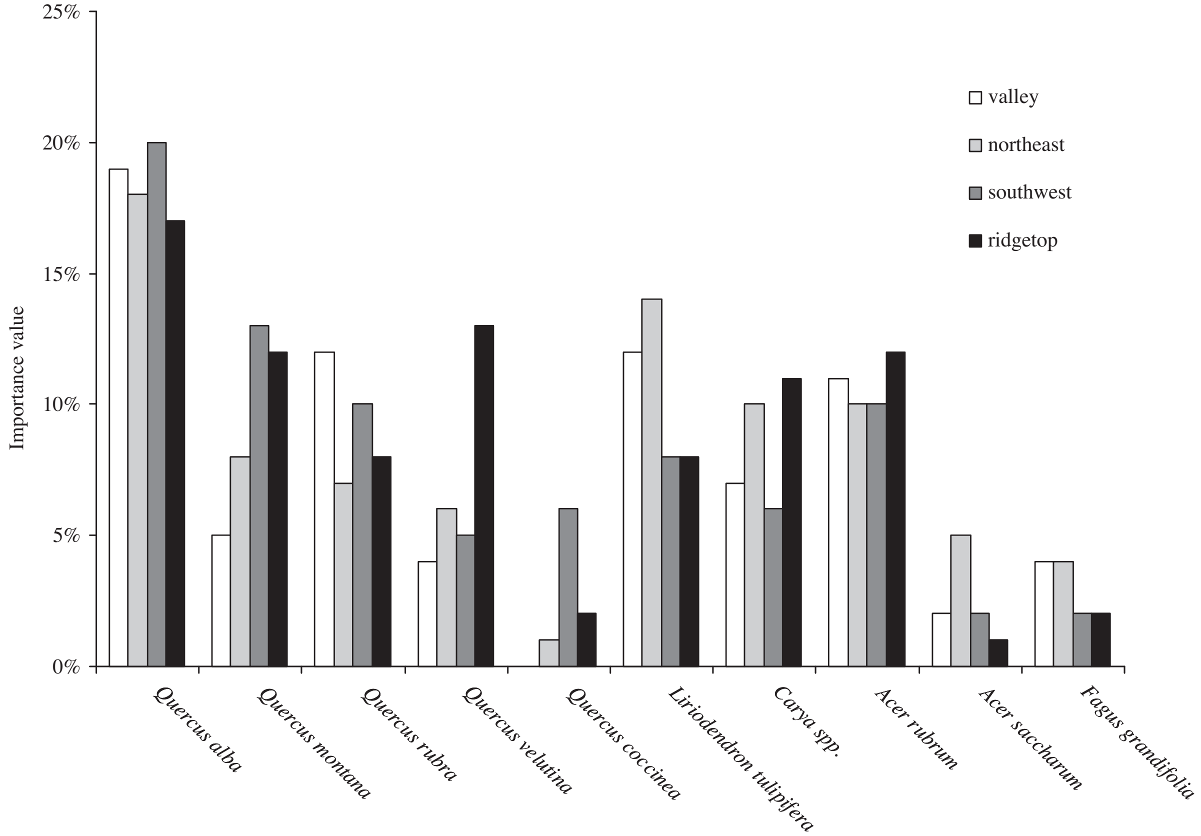

Fig. 1. Forest composition varied with topography in our study system. Importance of xeric adapted tree species was greatest on ridgetops and southwest-facing slopes, while mesophytic tree species were more important on northeast-facing slopes. Importance values from 278 random plots at unharvested sites in southeastern Ohio, 2007–2009.

2009 random plots were only sampled at CCWFMP study sites where the most intensive nest searching was conducted. To examine topography we measured slope (angle in degrees using a clinometer) and aspect (compass angle in degrees). Position on the slope was scored as valley, midslope or ridgetop (Morrissey et al., 2009 based on Bowersox and Ward, 1972; Weakland and Wood, 2005) using contour lines on topographic maps with valleys located <25 m from a stream and ridgetops located <25 m from the top of the ridge. Compass angle was scored from mesic northeast (315–135°) to xeric southwest (135–315°) facing aspects (Morrissey et al., 2009 based on Beers et al., 1966; Smalley, 1983). Due to differences in microclimate (Rosenberg et al., 1983), mesic northeast-facing slopes are generally more productive than xeric southwest-facing slopes (e.g. Fekedulegn et al., 2003; Graney, 1977). Topography was grouped into four categories for analysis: valley, northeast-facing midslope, southwest-facing midslope, and ridgetop. Although our study was in a predominantly forested landscape, several roads and power lines occurred adjacent to study sites, and we categorized edge nests as <100 m from an abrupt edge >8 m wide.

Point sampling with a variable radius plot was used to measure forest structure and tree species composition. Trees $\geqslant$10 cm dbh counted in a prism were multiplied by the prism factor (2.3× metric or 10× English) to calculate basal area. Trees were identified to species, and dbh was measured to the nearest centimeter to calculate basal area by tree species and size classes. Trees were grouped as xerophytic oaks (*Quercus montana*, *Q. velutina*, *Q. coccinea)* and mesophytic tree species (*Liriodendron tulipfera*, *Acer saccharum*, and *Fagus grandifolia*) (Braun, 1989, Figure 1). Species showing limited topographic association were examined separately: *Quercus alba*, *Quercus rubra*. *Carya* spp., and *Acer rubrum*. Oaks were dominant in the overstory in our study system and we also grouped white: *Q. alba* and *Q. montana* (sect. *Quercus*), and red oak species: *Q. rubra*, *Q. velutina*, and *Q. coccinea* (sect. *Lobatae*). Trees were classified as small (10–23 cm dbh), medium (23–38 cm dbh) and large (>38 cm dbh) (Martin et al., 1997). To

Table 2
Variables used in candidate microhabitat and nest placement models developed for analysis of nest-site selection and nesting success of canopy songbirds in southeastern Ohio.

Model	Variables	References
Topography	Position: valley, midslope northeast 315–135°, midslope southwest 135–315°, ridgetop; slope angle	Dettmers and Bart (1999), Hartman et al. (2009), Weakland and Wood (2005)
Canopy structure	Basal area: all trees, trees > 38 cm dbh, trees 23–38 cm dbh, trees 10–23 cm dbh	Hamel (2000), Mowbray (1999), Rodewald and James (1996)
Floristics	Basal area: xerophytic tree spp., mesophytic tree spp., white oak spp., red oak spp., *Q. alba*, *Q. rubra*, *Carya* spp., *A. rubrum*, grapevine	Bakermans (2008), George (2009), Rodewald and Abrams (2002)
Nest placement	Nest location (height, distance to bole, distance to foliage edge), nest support diameter, nest tree sp., nest tree size	Bakermans and Rodewald (2009), Beachy (2008), Newell and Kostalos (2007)
Concealment	Number of leaves around the nest	Johnson (1997) and Weidinger (2002)

Table 3
Canopy songbirds nested higher in sites more concealed by leaves in open canopy shelterwood stands than in unharvested mature second-growth in southeastern Ohio, USA, 2007–2009. Significance from a one-way ANOVA.

	Shelterwood			Unharvested			*P*-values	
Species	*n*	Hgt (m)	Leaves[a]	*n*	Hgt (m)	Leaves[a]	Hgt	Leaves
Eastern Wood-pewee	109	17.3 (0.4)	1.0 (0.2)	127	18.7 (0.4)	1.0 (0.1)	0.019	0.861
Yellow-throated Vireo	36	18.6 (0.9)	3.1 (0.5)	39	20.6 (0.8)	4.9 (0.7)	0.088	0.036
Blue-gray Gnatcatcher	48	19.5 (0.7)	3.2 (0.4)	57	21.7 (0.7)	4.5 (0.7)	0.027	0.107
Cerulean Warbler	48	19.8 (0.5)	5.1 (0.3)	115	20.3 (0.7)	6.7 (0.6)	0.740	0.013
Scarlet Tanager	74	17.7 (0.5)	5.6 (0.4)	99	19.0 (0.6)	6.9 (0.5)	0.106	0.029
Canopy-nesting guild	310	18.4 (0.3)	3.5 (0.2)	412	19.7 (0.3)	4.2 (0.2)	<0.001	0.021

[a] Number of leaves around the nest.

compare selection of the nest substrate to available trees, we calculated importance values of different tree species and size classes based on relative frequency, relative density, and relative basal area. Percent importance values were used and we focused on trees with values >2%; *Carya* spp. were pooled due to small numbers of individual species and difficult identification.

Additional data on nest placement were collected at nest plots for all nests monitored each year. We measured height of the nest, height of the nest substrate, base to the live crown, distance from the nest to the bole and distance from the nest to the nearest foliage edge (range finder or clinometer). Concealment can be difficult to measure objectively, especially for high nests, and leaves provided the main substrate concealing nests. To measure concealment we counted or estimated the number of leaves around the nest, assuming all leaves would conceal the nest from at least one direction (range: 0–12 leaves). Microhabitat at nest sites was compared to available habitat to identify important features selected by canopy songbirds. To characterize habitat available within the territory (Jones, 2001), a subset of random plots $\leqslant 100$ m from a nest were selected for each species using the ArcGis join function; a few random plots centered under open areas were excluded because canopy songbirds require trees for nest sites. Selecting random plots $\leqslant 100$ m from the nest represented potentially available habitat within the territory. Territories of our focal species generally range from 1 to 2 ha (Ellison, 1992; Hamel, 2000; McCarty, 1996; Mowbray, 1999; Rodewald and James, 1996), and maximum distance between renests in our study was 100 m.

2.5. Model selection and statistical analysis

An information–theoretic approach was used to compare different candidate models to explain nest-site selection and nesting success of canopy songbirds (Burnham and Anderson, 2002). Akaike's information criterion adjusted for small sample size (AIC_c) was used to rank models based on variance and the number of parameters. Models with $\Delta AIC_c < 2$ were considered equivalent, and models with $\Delta AIC_c < 10$ were considered to have some support. Model support was examined using Akaike weights, and models were compared relative to a null model containing no variables to examine importance of the association; we present supported models ranked better than a null model. We developed fifteen *a priori* candidate models examining topography, forest structure, and floristics based on previous information in the literature (Table 2). We focused on ecologically relevant variables with correlations <0.7. These models were used for both nest-site selection and nesting success. As location of the nest can be related to success (e.g. Johnson, 1997; Newell and Kostalos, 2007; Beachy, 2008), we also considered five models of nest placement (Table 2); nest height, distance to the bole, and distance to the foliage edge all described location of the nest within the tree and were included as one model. Additional factors in the model set included year, time of season, nest age, and edge category for a total of 26 candidate models examined to explain nesting success. Open and closed canopy stands were initially examined separately and then pooled. We present the pooled analysis and discuss any differences between open and closed canopy stands.

Program R-2.1 was used for statistical analysis (R Development Core Team, 2010). We used binomial generalized linear mixed-effects models with a logit link in the package lme4 (Bates and Maechler, 2010) for analysis of nest-site selection. Maximum likelihood (ML) methods were used to rank models, and we included forest and site as random intercepts to allow for correlation in habitat structure (Zuur et al., 2009). To examine factors associated with nesting success, we used the nest survival model in Program MARK 5.0 (White and Burnham, 1999) which allows for examination of covariates and a model selection approach (Dinsmore et al., 2002). Site was used as a grouping factor, and we did not standardize variables. Analysis was conducted in R using the RMark package (Laake, 2010). Recursive partioning with the package rpart (Therneau and Atkinson, 2010) was used to classify nest sites of the five canopy songbirds based on 14 microhabitat and nest placement variables used for analysis. ANOVA was used for topographic microhabitat and nest placement differences, and we used HSD Tukey *post hoc* tests with the multcomp package (Hothorn et al., 2008). Fisher's Exact tests for small sample size were used to compare topographic position of nest sites to available habitat within the territory. To examine selection of the nest substrate, percent importance values of tree species and tree size classes were multiplied by the total number of nests for each canopy species to obtain expected values and compared to actual number of nests using Fisher's Exact tests. Bonferroni adjusted *P*-values ($\alpha < 0.05$) were used in each analysis to control for repeated tests.

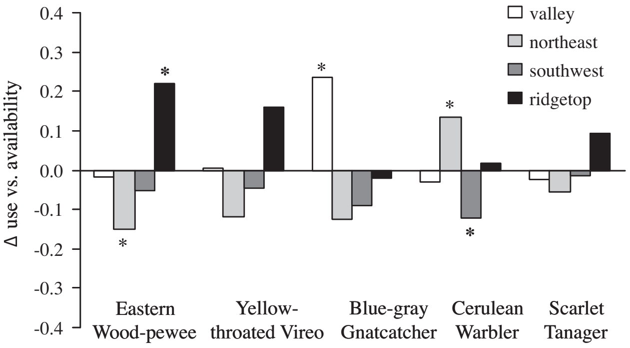

Fig. 2. Canopy songbird nest-site use versus availability of slope positions in upland mixed-oak forest in southeastern Ohio, 2007–2009. Asterisks indicate significant differences from Bonferroni adjusted Fisher's Exact tests ($P < 0.05$).

3. Results

3.1. Nest-site selection

Our study sites encompassed a range of upland habitat (28–35% northeast-facing midslope, southwest-facing midslope, and ridgetop), but only 8% of the lowest slope position. Shifts in forest composition with topography are typical in this region (Braun, 1989; Iverson et al., 1997), and in our system tree species such as *Q. velutina* increased on ridgetops, *Q. coccinea* increased on southwest-facing slopes, and *L. tulipfera* increased in valleys and on northeast-facing slopes (Fig. 1). Grapevines (*Vitus* spp.) were more abundant on northeast-facing slopes with 30% of plots at unharvested sites containing grapevine compared to 12% of plots on southwest-facing slopes ($z = -2.43$, $P = 0.01$). In addition, basal area of large trees was 26% higher on northeast-facing than on southwest-facing slope positions ($z = -2.73$, $P = 0.03$), although basal area of other tree size classes did not differ (all $P > 0.05$). Partial harvests were 16% less likely to be located on northeast-facing slopes than on southwest-facing slopes (Fisher's Exact test, $P < 0.01$).

We found 75–236 nests per species during the three years of the study with generally similar numbers of nests in both open and closed canopy stands. Overall, nests in open canopy stands averaged >1 m higher and were more concealed by leaves than in closed canopy stands (Table 3). In our system average crown ratio was 49%. Canopy species typically placed their nests in the crown, with average nest height ranging from 71% to 78% of the tree height, and nests averaged 44–68% of the distance from the bole to the foliage edge. Yellow-throated Vireos often suspended their nest near the bole of the tree, while Eastern Wood-pewees and Cerulean Warblers nested farthest out on the branch. The majority of pewee nests (>80%) were located in a fork with 50% of nests on dead branches. Other species used main branches at >50% (vireos always use forks), and only gnatcatchers occasionally nested on dead branches at 15%.

Consistent with nest height, all species selected large trees in higher proportion than available with 66–75% of nests in large trees compared to importance values of 47%, but avoided small trees with only 1–9% of nests in small trees compared to importance values of 26% (Fisher's Exact tests all $P < 0.05$). Species used medium trees as available with 20–28% of nests in medium trees compared to importance values of 27% (Fisher's Exact test all $P > 0.05$). Within the large tree size class, nests were located in canopy trees by dbh as available. Although *Q. alba* was dominant in our system, four canopy species selected this substrate more than twice as much as available, but avoided *A. rubrum* (Fig. 3). Blue-gray Gnatcatchers, Cerulean Warblers and Scarlet Tanagers avoided *Q. rubra* as a nest substrate and Eastern Wood-pewees avoided *Liriodendron tulipifera* (Fig. 3). The Yellow-throated Vireo was the only species that showed no apparent selection for nest substrates and used tree species in proportion to their availability (Fig. 3). Two vireo nests and three pewee nests were found in snags.

Nest site microhabitats differed from available habitat within the territory based on topography, tree size, and floristics. Topography was important for Eastern Wood-pewees, Blue-gray Gnatcatchers and Cerulean Warblers (Table 4, Fig. 2). Sixty percent of pewee nests were located on ridgetops and pewees selected microhabitats with 51% higher basal area of xerophytic oaks species than

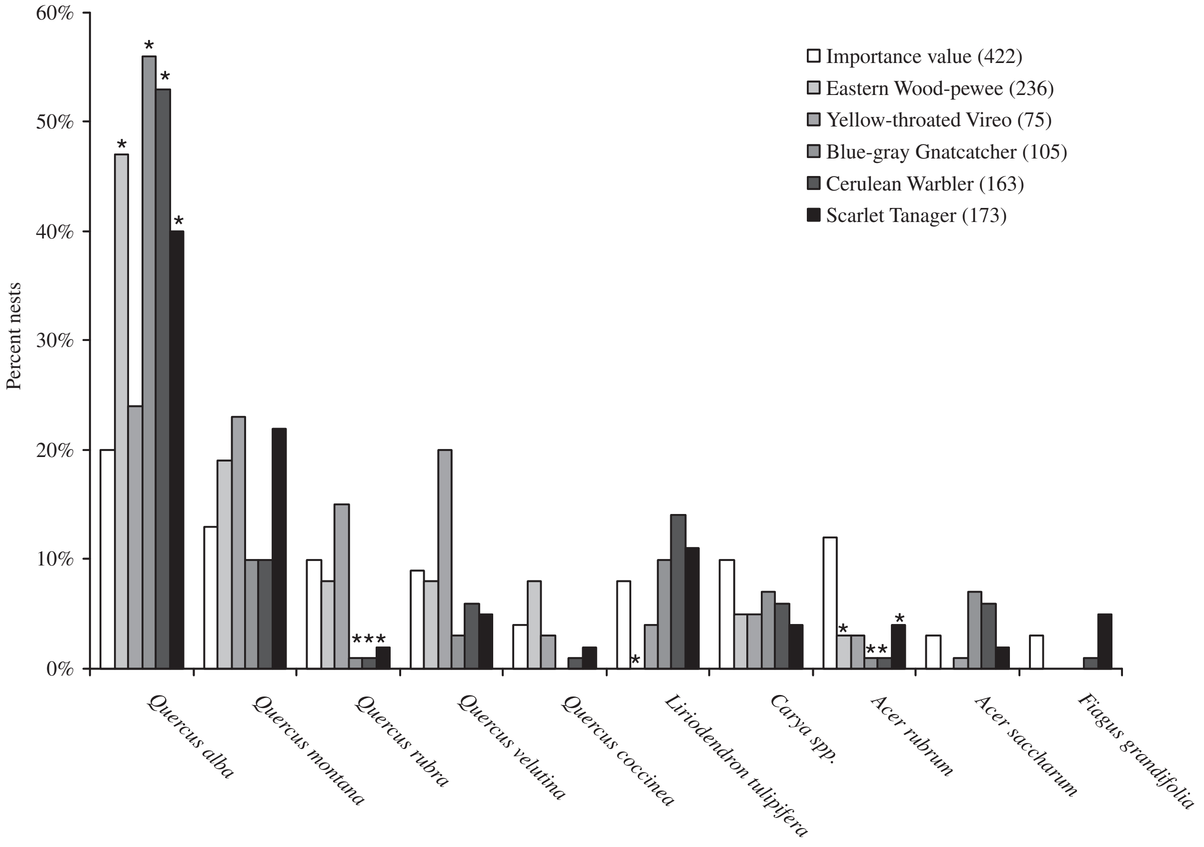

Fig. 3. Tree species used by canopy songbirds for nest sites versus availability. Importance values based on relative frequency, relative density, and relative basal area were calculated from random plots $\leqslant$100 m from any nest. Sample sizes in brackets indicate number off nests and number of random plots. Asterisks indicate significant differences from Bonferroni adjusted Fisher's Exact tests ($P < 0.05$).

available, especially *Q. montana*. Yellow-throated Vireos also selected microhabitats with 56% higher basal area of xerophytic oaks and, although topographic selection was not apparent within the territory, 65% of vireo nests were located on ridgetops. On the other hand, Cerulean Warblers selected northeast-facing slopes, and nest sites had 17% higher basal area of large trees, 92% more grapevine, but 43% lower basal area of *A. rubrum* than available. In closed canopy stands basal area of medium trees was the top model for Ceruleans, and overall nest sites had 20% lower basal area of medium trees than available. While Ceruleans selected mesic microhabitats, pewees avoided northeast-facing slopes, mesophytic tree species, and grapevine in closed canopy forest. Conversely, gnatcatchers preferred valleys with 34% of nests at the lowest topographic position. In our upland system, gnatcatcher avoidance of red oak species, especially *Q. rubra*, seemed to be the dominant factor in nest-site selection, and gnatcatchers nested in microhabitats with 66% lower basal area of *Q. rubra* than available. The Scarlet Tanager was the only species that showed no apparent nest-site microhabitat selection. In open canopy stands four canopy species selected microhabitats with white oak species, and nest sites had 33–50% higher basal area of white oaks than available (only Yellow-throated Vireos showed no apparent selection in open canopy stands).

Table 4

Comparison of candidate models to explain nest-site selection and nesting success of canopy songbirds across open and closed canopy forest in southeastern Ohio, 2007–2009. Nest-site selection is from binomial mixed-effects models with the lme4 package and nest success is from the RMark package in R.

Species	Model	k	AIC$_c$	Δ_i	ω_i
Eastern Wood-pewee (236 nests and 369 random plots)					
Selection	Topography	4	781.70	0.00	0.52
	Xerophytic oak spp.	4	781.85	0.15	0.48
Success	{Time of season} Nest tree sp.	3	840.50	0.00	0.55
	{Time of season} Red oak spp.	3	843.64	3.14	0.12
	{Time of season} *Q. rubra*	3	845.82	5.31	0.04
	{Time of season} Slope	3	846.09	5.59	0.03
	{Time of season} *Q. alba*	3	846.31	5.81	0.03
	{Time of season} Xerophytic oak spp.	3	846.47	5.97	0.03
	{Time of season}	2	847.02	6.52	0.02
Yellow-throated Vireo (75 nests and 221 random plots)					
Selection	Xerophytic oak spp.	2	327.72	0.00	0.96
	Mesophytic tree spp.	2	335.46	7.74	0.02
Success	Year	2	296.03	0.00	0.09
	Carya spp.	2	296.38	0.35	0.07
	Q. rubra	2	296.44	0.41	0.07
	Null	1	296.48	0.44	0.07
Blue-gray Gnatcatcher (105 nests and 213 random plots)					
Selection	Red oak spp.	2	380.35	0.00	0.96
	Q. rubra	2	387.15	6.81	0.03
	Topography	4	389.79	9.44	0.01
Success	Nest support	2	398.06	0.00	0.08
	Null	1	398.32	0.25	0.07
Cerulean Warbler (163 nests and 238 random plots)[a]					
Selection	Topography	4	531.89	0.00	0.69
	Trees > 38 cm dbh	2	534.16	2.27	0.22
	A. rubrum	2	537.96	6.07	0.03
	Trees 23–38 cm dbh	2	539.70	7.81	0.01
	Grapevines	2	540.42	8.52	0.01
	Mesophytic tree spp.	2	541.28	9.39	0.01
Success	Xerophytic tree spp.	2	493.43	0.00	0.14
	Red oak spp.	2	493.93	0.51	0.11
	Nest age	2	494.13	0.70	0.10
	Large trees	2	494.24	0.81	0.09
	Topography	2	494.78	1.35	0.07
	Q. rubra	2	495.01	1.58	0.06
	Nest tree size	2	495.11	1.69	0.06
	Time of season	2	495.95	2.52	0.04
	Carya spp.	2	496.17	2.75	0.04
	Grapevines	2	496.18	2.76	0.04
	Basal area	2	496.34	2.91	0.03
	Slope	2	496.43	3.00	0.03
	Null	1	496.53	3.11	0.03
Scarlet Tanager (173 nests and 348 random plots)					
Selection	*Carya* spp.	2	666.33	0.00	0.19
	Null	1	667.55	1.22	0.11
Success	Concealment	2	544.17	0.00	0.77
	Nest support	2	547.57	3.40	0.14
	Year	2	550.95	6.78	0.03
	Nest age	2	552.31	8.14	0.01
	Red oak spp.	2	552.61	8.45	0.01

[a] Sample size for Cerulean Warbler nesting success 133 nests.

Nest sites differed among canopy species in terms of concealment of the nest, diameter of the support branch, topographic position on the slope, and basal area of large trees (Fig. 4). Yellow-throated Vireos, which build a hanging cup in the fork of a small twig, separated from the other canopy species based on the nest support. Eastern Wood-pewees separated from Cerulean Warblers and Scarlet Tanagers based on concealment of the nest while Blue-gray Gnatcatchers separated by topographic position on the slope. Cerulean Warblers separated from Scarlet Tanagers based on basal area of large trees around the nest.

3.2. Nesting success

Nesting success was low with daily survival rates (DSR) of 0.951 ± 0.002 S.E. translating to a 30% success rate for a 24 day nesting cycle. DSR of individual species ranged from 0.929 ± 0.008 S.E. for Yellow-throated Vireos to 0.965 ± 0.002 S.E. for Eastern Wood-pewees (15–36% success; nesting cycles of individual species ranged from 21–29 days). Overall, nesting success was similar between open and closed canopy stands for all species (Newell and Rodewald, in press). Eastern Wood-pewees began nesting three weeks after the other species and continued to renest through the end of July. Success improved across the season (Fig. 5a) with DSR of 0.978 ± 0.008 S.E or 56% success ($n = 87$) for late season nests compared to 0.958 ± 0.005 S.E. or 32% ($n = 169$) success for nests initiated before the third week of June when species such as the Cerulean Warbler and Blue-gray Gnatcatcher generally stopped nesting (Scarlet Tanagers and Yellow-throated Vireos continued to nest through the first week of July). With model weights of 100% compared to a null model we used time of season as a base model for pewee nesting success. For Cerulean Warblers predation tended to increase while birds were feeding young (Table 4, Fig. 5b) with predation 11% higher during the nestling phase, and daily survival rates of nestlings 0.916 ± 0.013 S.E. compared to 0.937 ± 0.008 S.E. daily survival of eggs. On the other hand, for Scarlet Tanagers with relatively large conspicuous nests, predation occurred early in the nesting cycle and success was positively associated with leaf concealment as well as size of the support branch (Table 4, Fig. 5c). Blue-gray Gnatcatcher nesting success was also positively associated with size of the support branch in closed-canopy stands, while in open canopy stands Cerulean Warbler and Scarlet Tanager nesting success decreased later in the breeding season.

Microhabitat models to explain nesting success were generally less well supported than models to explain nest-site selection (Table 4). Floristics seemed to be the most consistent factor across species. For Eastern Wood-pewees nesting success was only 8% (0.917 ± 0.021 S.E. DSR, $n = 18$) in *Q. velutina* compared to 33–42% success for nests in other oak species (0.962 ± 0.008–0.970 ± 0.009 S.E. DSR, $n = 18–110$). In addition success was negatively associated with basal area of pooled red oak species around the nest (Table 4, Fig. 6a), with both *Q. velutina* and *Q. rubra* driving this association. Scarlet Tanagers showed a similar negative association with red oak species in general. Floristics may also have been important for Cerulean Warblers, although associations were

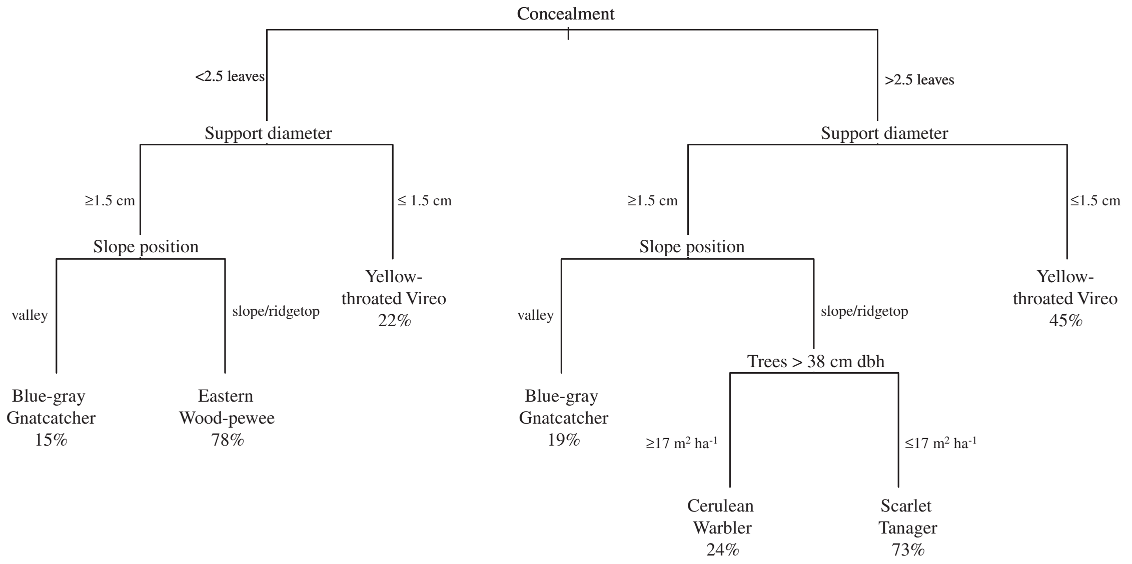

Fig. 4. Classification tree for nest sites of canopy songbirds in southeastern Ohio, 2007–2009. Percentage of nests classified are below the species name.

complicated and varied among forests. Overall Cerulean success was negatively associated with large xerophytic or red oak species, with both *Q. montana* and *Q. rubra* driving these associations (Table 4, Fig. 6d); variables in other top models were correlated with these variables ($r_s > 0.30$). Associations were driven by ZSF which had twice the basal area of xerophytic and red oak species compared to VFEF (Table 1). At ZSF nesting success was only 8% in closed canopy forest (0.896 ± 0.021 S.E. DSR, $n = 27$) compared to 19% success in shelterwoods (0.931 ± 0.014 S.E. DSR, $n = 31$). At VFEF nesting success was 22% in closed canopy forest (0.937 ± 0.010 S.E. DSR, $n = 64$) and few Ceruleans nested in open canopy stands. In closed canopy forest at VFEF Cerulean nests were half as successful in large trees at 14% (0.919 ± 0.015 S.E. DSR, $n = 39$) compared to 37% success in small and medium trees (0.957 ± 0.012 S.E. DSR, $n = 25$). Overall, none of the models examined explained nesting success for the two less abundant canopy species, Yellow-throated Vireos and Blue-gray Gnatcatchers, with top models ranked $\Delta \text{AIC}_c < 2$ compared to a null model (Table 4).

For three canopy species individually, nesting success was negatively associated with red oak species. Yellow-throated Vireos, which used red oaks as available for nest sites, had extremely low nesting success, and Blue-gray Gnatcatchers avoided areas with red oaks (Fig. 6a–e). *Post hoc* we examined relationships among different oak species and nesting success across the canopy guild. Pooling nests of all species, daily survival rates were negatively associated with basal area of red oak species around the nest ($\beta = 0.028 \pm 0.009$ S.E., 95% C.I. −0.046 to −0.010) (Fig. 6f), mainly the two common red oak species in our system, *Q. velutina* and *Q. rubra* (Table 5), although these two oaks were not correlated with each other at nest sites ($r_s = -0.03$).

4. Discussion

Our results highlight the combined role in of topography, canopy structure, and floristics in nest-site selection and nesting success of canopy songbirds. In our upland system topography was the best indicator of nest-site microhabitat selection, and canopy songbirds collectively selected structural and floristic characteristics associated with a favored topographic microclimate. For example, the Cerulean Warbler favored productive northeast-facing slopes characterized by large trees and grapevines. For a guild with similar nest height, topographic position and nest construction (e.g. concealment and type of nest/support) were the main factors differentiating among species. As expected from nest height, the majority of canopy nests were located in large trees. Our results provide evidence that floristics may be important. Whereas *Q. alba* was preferred for nest sites, red oak species such as *Q. velutina* and *Q. rubra* where either avoided or were negatively associated with nesting success. Causes for observed differences among oak species remain to be determined.

Topography played the strongest role in structuring nest site selection of canopy songbirds. Eastern Wood-pewees favored xeric ridgetops, as previously documented in the region (Dettmers and Bart, 1999). In Illinois pewees were also abundant on ridgetops and effects of partial harvesting were only apparent in ravines (Robinson and Robinson, 1999); however, in our upland system abundance was higher in shelterwoods than in unharvested stands (Newell and Rodewald, in press). In contrast, Blue-gray Gnatcatchers selected valleys, and this species may reach its highest abundance in riparian areas (Ellison, 1992). Aspect was important for Cerulean Warblers which favored productive northeast-facing slopes as previously suggested by others (Hartman et al., 2009; Wood et al., 2006). Interestingly, the two canopy species differing in nest construction, the Yellow-throated Vireo which builds a hanging cup nest and the Scarlet Tanager which builds a loose woven structure, showed no clear topographic associations. Although vireos generally nested on ridgetops in our system, others studies show vireos can be abundant in bottomland hardwood forest (Norris et al., 2008; Rodewald and James, 1996).

Forest composition and structure change with topography, which might explain nest-site preferences. Several canopy species selected microhabitats with xerophytic oak species found on ridgetops in the region. Cerulean Warbler selection for northeast-facing slopes may relate to site productivity, and trees generally grow best and reach their largest size on northeast-facing slopes (Fekedulegn et al., 2003; Graney, 1977). Mesophytic plant communities found on northeast-facing slopes may be important. In our upland system xerophytic oak species were negatively associated with nesting success. Perhaps part of evolutionary adaptation to a particular forest microclimate, Cerulean Warblers use grapevines for nest construction (Bakermans and Rodewald, 2009), and grapevines are also more abundant on northeast-facing slopes (Morrissey et al., 2009).

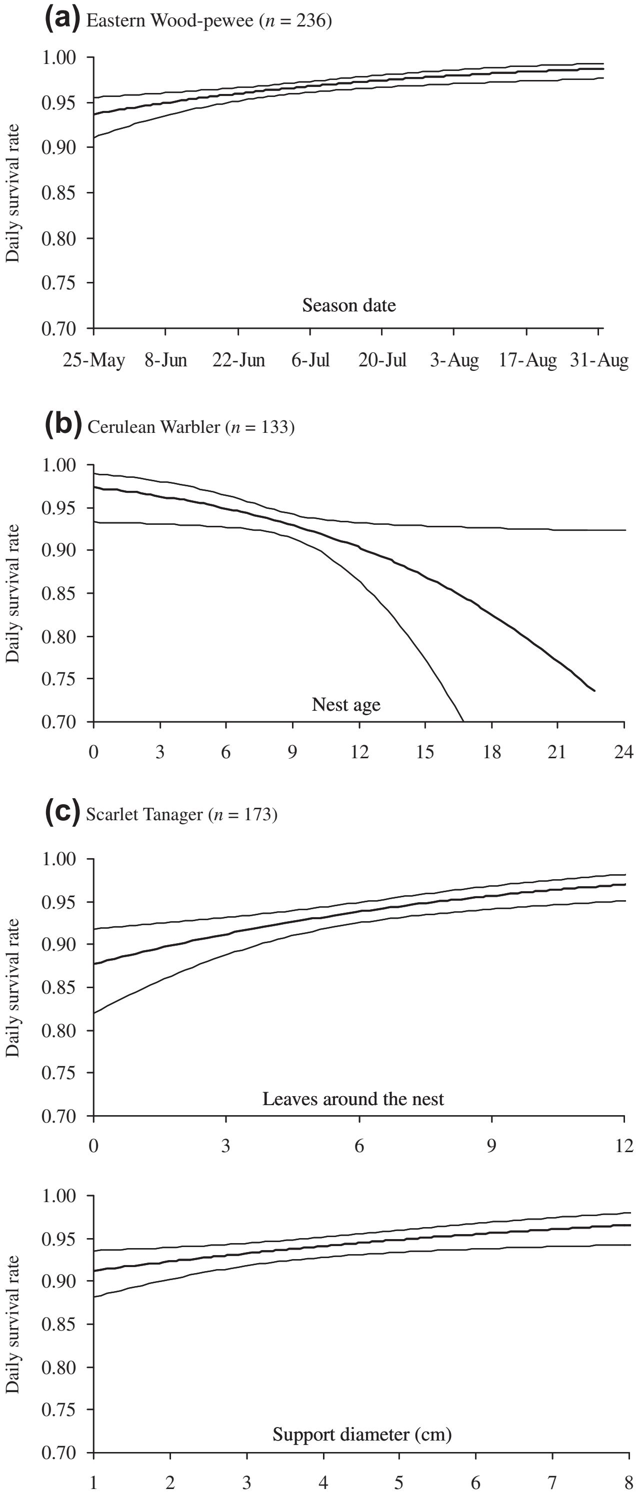

Fig. 5. Factors related to daily survival rates of canopy songbird nests in southeastern Ohio, 2007–2009. Eastern Wood-pewee success increased during the breeding season, predation was highest during the nestling phase for Cerulean Warblers, and Scarlet Tanager success was positively associated with concealment and size of the support branch. Lines indicate means and 95% confidence intervals.

Canopy songbirds nested in both open and closed canopy stands, although nests in shelterwoods were overall higher and better concealed by leaves than in unharvested stands. Nest placement can vary depending on the structure of the forest (e.g. Artman and Downhower, 2003). However, microhabitat selection was similar across stands, even though abundance was higher in open than in closed canopy stands (Newell and Rodewald, in press). Basal area, which accounts for both number of trees and size in a single measurement, failed to explain nest-site selection for any canopy species. Birds apparently did not differentiate between open and closed canopy stands when selecting nest sites: territories overlapped harvest edges, and pairs often renested in either stand type. Our finding that Cerulean Warblers at unharvested sites selected nest sites in areas with fewer medium trees, however, tends to support the importance of older forest with broken canopies documented in other studies (e.g. Bakermans and Rodewald, 2009; Hamel, 2000; Jones et al., 2001). In addition, Cerulean Warblers were twice as abundant in shelterwoods as in unharvested stands in one forest (Newell and Rodewald, in press). Similar to increased tree growth rates on productive northeast-facing slopes, canopy openings competitively release trees (e.g. Lorimer and Frelich, 1989).

Although importance of oaks as wildlife habitat has often been generalized across the *Quercus* genus, we found strong differences among oak species. Almost all canopy species favored *Q. alba* as a nest substrate. Bakermans (2008) also found Cerulean Warblers preferentially select *Q. alba* for nest sites in this region while canopy nests have often been documented in *Q. alba* (Ellison, 1992; McCarty, 1996; Mowbray, 1999). Interestingly the Yellow-throated Vireo, the only species not preferring any tree species, suspends its nest from the fork of a small twig, while the four other species place their nests in a fork, or on a branch. Selection of *Q. alba* for nest sites could relate to branch architecture, such as rough bark or suitable forks for nest attachment. However, preferences for *Q. alba* also reflect what some argue represents pre-European settlement forests (Abrams, 2003; Nowacki and Abrams, 2008). Importance values of *Q. alba* in Ohio prior to European settlement have been estimated as high as 40% (Dyer, 2001). In Europe several Paridae species are well known to depend on spring lepidopteran larvae found on white oak species to feed their nestlings (Perrins, 1991). Individuals lay larger clutches and nestlings are in better condition in proximity to oaks or in oak forests (Atiénzar et al., 2010; Wilkin et al., 2009). However, the extent to which canopy songbird nest site preferences reflect tree morphology, or other plant–animal interactions remains to be determined.

To our knowledge, this study provides the first evidence that red oak species may be generally avoided for nesting and could be negatively associated with nesting success. Bakermans (2008) also suggested Cerulean Warblers avoid *Q. rubra* for nest sites in this region. Recent work has found several forest species, including the Cerulean Warbler and Scarlet Tanager, avoid red oak species for foraging as well (George, 2009). This match between foraging and nest site avoidance is interesting, given that the two species which did not avoid *Q. rubra* for nest sites were either an aerial flycatcher (Eastern Wood-pewee) or a less consistent foliage gleaner (Yellow-throated Vireo). Vireos only obtain about 30% of prey from foliage (Rodewald and James, 1996), and show no apparent tree species foraging preferences (Gabbe et al., 2002).

Moisture gradients could play a role in the negative associations between red oaks species and nesting success found in our study. Although the model containing all red oak species had the strongest support, there was some support for individual oak species such as *Q. velutina* found on xeric ridgetops. Hotter, drier microclimates in upland areas may be used by predators such as the black rat snake (*Elaphe obsoleta*) (Carfagno and Weatherhead, 2006), and a black rat snake was directly observed depredating a Cerulean Warbler nest 28 m up in a large *Q. velutina* tree at ZSF (F. Newell, *personal observation*). Using parental behavior to find nests (Mullin and Cooper, 1998), snakes are more likely to depredate nests during the nestling phase (Benson et al., 2010; Stake et al., 2005), an association we found for Cerulean Warblers.

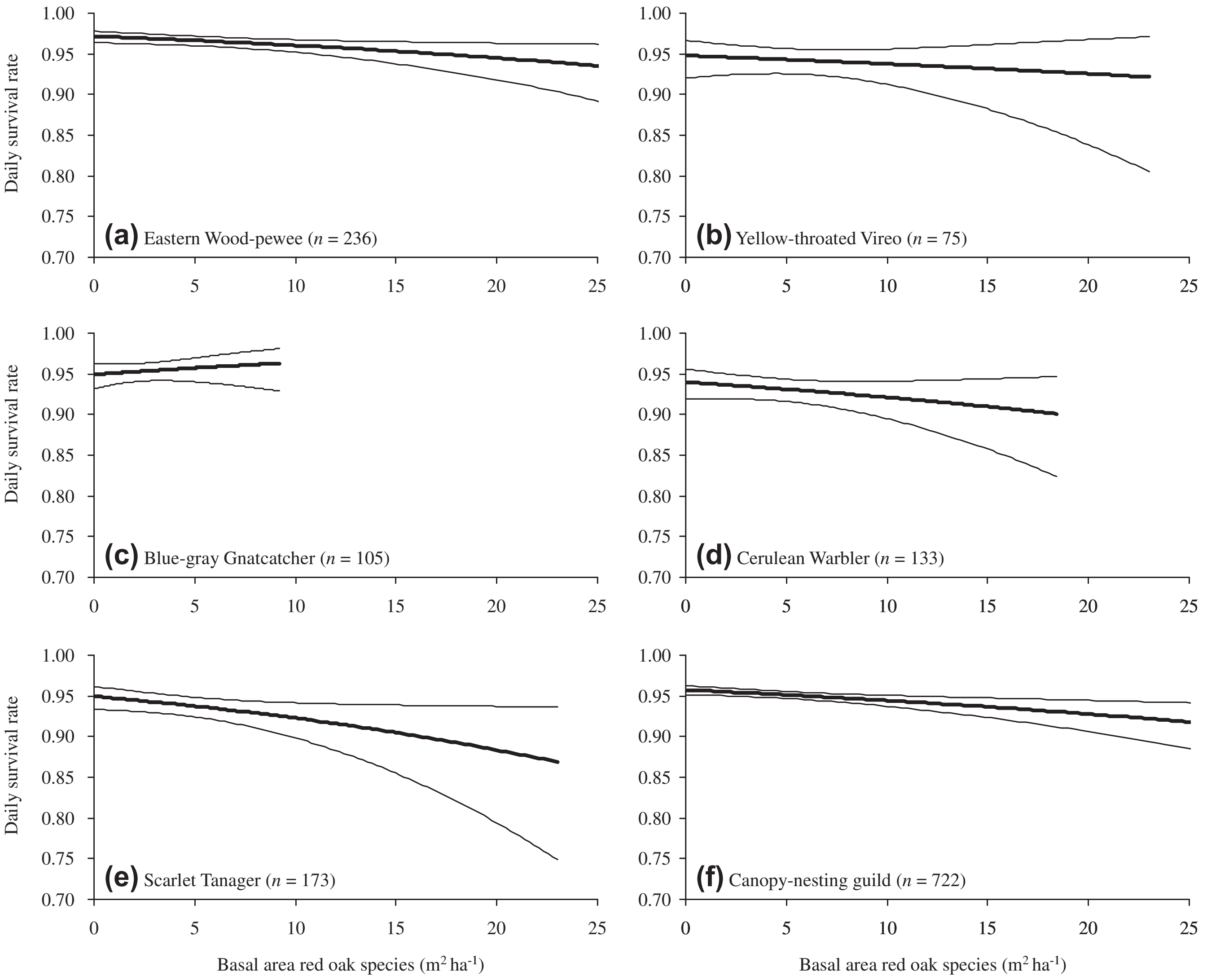

Fig. 6. Relationship between daily survival rates of canopy songbird nests and basal area of red oak species in southeastern Ohio, 2007–2009. Models were supported for Eastern Wood-pewees, Cerulean Warblers, and Scarlet Tanagers. Yellow-throated Vireos had extremely low nesting success, and Blue-gray Gnatcatchers avoided areas with red oaks. Pooling across canopy species success was negatively associated with basal area of red oak species, especially *Q. velutina* and *Q. rubra*. Lines indicate means and 95% confidence intervals.

Table 5
Post hoc comparison of different oak species to explain nesting success of canopy songbirds (722 nests) in southeastern Ohio, 2007–2009. Basal area of red oaks was negatively associated with success across canopy species and canopy openness.

Model	k	AIC$_c$	Δ_i	ω_i
Red oak spp.	2	2624.77	0.00	0.72
Q. velutina	2	2628.47	3.70	0.11
Q. rubra	2	2628.85	4.08	0.09
Null	1	2631.80	7.03	0.02
Q. alba	2	2632.53	7.76	0.01
Xerophytic oak spp.	2	2632.60	7.83	0.01
White oak spp.	2	2632.69	7.92	0.01
Q. coccinea	2	2633.72	8.95	0.01
Q. montana	2	2633.78	9.01	0.01

Blue Jays (*Cyanocitta cristata*) were likely another important nest predator in our system, which may have contributed to low nesting success even in a predominantly forested region. We directly observed Blue Jays depredating a Cerulean Warbler nest during incubation (F. Newell, *personal observation*), as well as Yellow-throated Vireo and Scarlet Tanager nests both with nestlings (F. Newell and T. Johnson, *personal observations*). Blue Jays, as well as an American Crow (*Corvus brachyrhynchos*), were seen on four different occasions looking into failed nests of several canopy species, which they may have depredated. Birds regularly gave alarm calls in the presence of Blue Jays, and Eastern Wood-pewees actively defended the nest area, dive-bombing and chasing away jays. In addition to confirmed nest predators, other less commonly observed predators in our system included Eastern Chipmunks (*Tamias striatus*), Eastern Gray Squirrels (*Sciurus carolinensis*), and Raccoons (*Procyon lotor*), as well as several raptor and owl species.

In some cases prey resources can interact with predators to indirectly affect reproductive success through anti-predator behavior (Schmidt, 1999; Rastogi et al., 2006; Zanette et al., 2006). Avoidance of red oak species for foraging (George, 2009) may indicate differences in arthropods. Although studies have found similar numbers of lepidopteran larvae among tree species (Butler and Strazanac, 2000; Summerville et al., 2003; Turčani et al., 2010), individual Lepidopera species often specialize on host trees. For example, tree species such as *Q. alba* can contain five times the number of leaf-tying Lepidoptera compared to other oak species (Marquis and Lill, 2010). Leaf chemistry also can influence herbivorous insects, including nitrogen (Koricheva et al.,

1998) and tannins (Feeny, 1970; Rossiter et al., 1988; Schultz and Baldwin, 1982), and tannins can increase on southwest-facing slopes in several oak species (Forkner and Marquis, 2004). If preferred prey were reduced on red oak species, birds might have to leave the nest unattended as they invest more effort in foraging away from the nest (Stauss et al., 2005; Tremblay et al., 2005). Further work is needed to understand tree species preferences and associations to identify if management for individual tree species benefits birds.

In most cases nest-site preferences did not match nesting success in our study, although relationships between preferences and fitness may vary with spatial scale and metric of fitness (Chalfoun and Martin, 2007). Examples such as the Eastern Wood-pewee nesting later in the season with increased success, and Scarlet Tanager success associated with nest concealment, provide evidence for evolutionary adaptations to increase fitness. However, for species like the Cerulean Warbler, habitat features associated with nesting success varied among forests, and topographic, structural, and floristic preferences did not predict nesting success for any canopy species. Microhabitat preferences of canopy songbirds could relate to foraging behavior and/or preferred prey resources as opposed to predation risk. Although we did not study foraging behavior, there were clear interspecific differences among the canopy guild, which could structure microhabitat preferences for species with similar nest height. Further work is needed to understand underlying factors driving topographic, structural and floristic associations of canopy songbirds.

5. Management implications

This study highlights the importance of considering topographic microclimate in forest management decisions. Our results support the protection of stands with large trees, grapevines and broken canopies, such as found on northeast-facing slopes, for conservation of the severely declining Cerulean Warbler. We recommend partial harvests retain sufficient canopy trees for canopy songbirds to use for foraging and nest sites. Association between canopy songbirds and oaks reaffirms the value of current management efforts to promote oak regeneration, although some new insight from our work indicates differences among oak species. Managers should make special effort to retain and promote regeneration of *Q. alba*. Red oak species may be less beneficial, but further work is needed to understand causes for canopy songbird avoidance of red oak species and negative associations with nesting success found in this study.

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