CHAPTER SEVEN

Golden-winged Warbler Nest-Site Habitat Selection*

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Abstract. Avian habitat selection occurs at multiple spatial scales to incorporate life history requirements. Breeding habitat of Golden-winged Warblers (*Vermivora chrysoptera*) is characterized by largely forested landscapes containing natural or anthropogenic disturbance elements that maintain forest patches in early stages of succession. Breeding habitat occurs in a variety of settings, including shrub and forest swamps, regenerating forests following timber harvest, grazed pastures, and reclaimed mined lands. We identified structural components of nest sites for Golden-winged Warblers by measuring habitat characteristics across five states (North Carolina, New York, Pennsylvania, Tennessee, and West Virginia) in the Appalachian breeding-distribution segment and two states (Minnesota and Wisconsin) in the Great Lakes breeding-distribution segment. We measured habitat characteristics at the nest-site scale with a series of nested plots characterizing herbaceous vegetation (grasses and forbs), woody shrubs and saplings, and overstory trees. We measured similar variables at paired random plots located 25–50 m from the nest within the same territory to evaluate selection. We used conditional logistical regression to identify which parameters were important in habitat selection and Simple Saddlepoint Approximation (SSA) to aid in management interpretation of identified parameters for each study site. Study site was an important determinant for which parameters were significant in nest-site selection, although selection for some parameters was consistent across sites. The amount of woody cover at the nest-site scale was consistently present in the top nest-site selection models across sites, although the direction of the relationship was not the same across all sites. We also identified grass, forb, woody cover, and vegetation density as important components of Golden-winged Warbler nest-site selection. Based on SSA, we identified vegetation thresholds to aid in designing habitat management prescriptions to promote creation or restoration of Golden-winged Warbler nesting habitat across the eastern portion of their breeding distribution.

Key Words: habitat, nest-site selection, saddlepoint approximation.

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Avian habitat selection is envisioned to occur in a hierarchical fashion from a species' breeding distribution, to the landscape selected by a population, to the territory selected by an individual male, and ultimately to the nest site selected by an individual female (Johnson 1980). Habitat selection by birds is typically assumed to be adaptive such that fitness is higher in selected habitats because of increased probability of successful reproduction, survival, or both (Martin 1998). If nest-site characteristics can be identified and linked to fitness then managers can create or restore sites with these characteristics and a population may respond positively. Population responses may be in the form of colonization of these sites, successful reproduction on these sites, and enhanced survival of adults and fledglings once the initial decision to establish a territory and build a nest has been made.

We documented patterns of nest-site selection in Golden-winged Warblers (*Vermivora chrysoptera*) to help guide management prescriptions intended to ensure availability of nest sites within the larger context of the species' breeding habitat. Golden-winged Warbler populations have declined significantly across most of their breeding range and are considered a species of international conservation concern (Buehler et al. 2007, USFWS 2008, Sauer et al. 2012). In turn, concern about declining populations has led to a major effort to increase the availability of quality breeding habitat on public and private lands (e.g., Bakersman et al. 2011, Golden-winged Warbler Working Group 2013).

Golden-winged Warblers nest across a broad range of conditions (Confer et al. 2011), including young forests and edges of adjacent mature forest stands following timber harvest (Klaus and Buehler 2001, Kubel and Yahner 2008, Roth et al. 2014, Streby et al. 2014), reclaimed surface mines (Bulluck and Buehler 2008, Patton et al. 2010), shrub wetlands (Rossell et al. 2003), swamp forests (Confer et al. 2010), abandoned fields (Confer et al. 2003), power line rights-of-way (Kubel and Yahner 2008), and grazed, high-elevation pastures (Aldinger 2010, Aldinger and Wood 2014). Consistent habitat characteristics used across the breeding distribution include patches of herbaceous cover (grasses and forbs), shrubs and saplings, and mature forest edges. The unique combination of habitat characteristics associated with nest sites has been described for individual studies, but we are not aware of any study comparing habitat characteristics across multiple sites to determine which habitat characteristics are consistent across the breeding distribution. The identification of common characteristics of habitat selection is important for development of distribution-wide conservation strategies. In the absence of such consistent characteristics, habitat management strategies for Golden-winged Warblers may have to be tailored to conditions found on each individual management site or locale where specific habitat characteristics are consistently associated with nest sites.

We designed this study to examine nest-site selection by Golden-winged Warblers across their breeding distribution and across a broad range of ecological conditions in five states in the Appalachian breeding-distribution segment and two states (Minnesota and Wisconsin) in the Great Lakes breeding-distribution segment as outlined in the Golden-winged Warbler Conservation Action Plan (A. M. Roth et al., unpubl. plan; Figure 7.1). The goal of our study was to identify key habitat characteristics associated with nest sites and to compare how nest-site selection varied across the range of study sites we evaluated. Furthermore, we identified threshold values for selection of specific habitat characteristics to aid in development of habitat management prescriptions for Golden-winged Warblers.

METHODS

Study Areas

We selected Golden-winged Warbler breeding sites in five states (North Carolina, New York, Pennsylvania, Tennessee, and West Virginia) in the Appalachian breeding-distribution segment and two states (Minnesota and Wisconsin) in the Great Lakes breeding-distribution segment (Figure 7.1) in vegetation cover types representative of those described in the literature (summarized in Confer et al. 2011). Forest-type descriptions generally follow Braun (2001) unless otherwise noted. Study areas featured recent (<25 years), ongoing, or both recent and ongoing disturbances that created patches of young forest in a predominantly forested landscape. In general, study sites were a mosaic of grasses, forbs, low shrubs, saplings, and few canopy trees surrounded by intact forest.

Study sites at Tamarac National Wildlife Refuge (46.967°N, 95.650°W; 425–500 m in elevation) in Becker County, Minnesota were located at the prairie-forest transition and were comprised

Figure 7.1. Location of individual study sites included in nest-site selection studies of Golden-winged Warblers with distinct conservation management units delineated in gray (Adapted from Roth et al., unpublished report).

of second-growth, moderately closed-canopy aspen (*Populus* spp.) and oak (*Quercus* spp.) forest, interspersed with regenerating forest stands and wetlands. Two upland regenerating forest stands included in this study were created by a combination of gravel removal (one stand), timber harvests, and prescribed burns. Low-quality soils on these stands resulted in a relatively slow rate of succession.

Study areas in Wisconsin were nine aspen-dominated forest stands (45.717°N, 89.533°W; 473–508 m) that had been harvested with varying densities and species of retained canopy trees in Oneida and Vilas counties. Timber harvests involved removal of all aspen and most other tree species except oak (*Quercus* spp.) and pine (*Pinus* spp.) marked to be retained. The landscape was dominated by northern hardwood forests.

Study areas in North Carolina were located within the Amphibolites (36.400°N, 81.700°W) and Roan Mountain (36.100°N, 82.133°W) Important Bird Areas in Watauga County and extending into Carter County, Tennessee at elevations of 880–1,500 m. A combination of livestock grazing and mechanical brush-removal maintained young forest stands at these sites. Golden-winged Warbler breeding habitat at these study areas was characterized by grass-forb-dominated ground-level vegetation with hawthorn (*Crataegus* spp.) providing the primary woody structure, adjacent to mixed-mesophytic and northern hardwood forests.

The study area in New York was at Sterling Forest State Park (41.183°N, 74.233°W; 245–365 m) in the Hudson Highlands of Orange County. We found Golden-winged Warblers nesting in three cover types: managed upland utility rights-of-way, managed upland hardwood forests, and swamp red maple (*Acer rubrum*)-dominated forests. Sterling Forest is part of the largest forest-dominated tract remaining in the New York–New Jersey Highlands.

We included three study areas in Pennsylvania. Bald Eagle State Park (41.033°N, 77.650°W; 210–245 m) in Centre County consisted of a mosaic of fragmented forests, shrublands, managed grasslands, and powerline rights-of-way. Agricultural and residential land uses were interspersed among the northern hardwood and oak-hickory forests. Sproul State Forest (41.233°N, 77.083°W; 600–620 m) in Centre and Clinton counties was comprised of extensive tracts of northern hardwood and dry oak forests with little human land use. Recent timber harvests since 1990 and a 4,000-ha burn in 1990 led to stands of young forest on the area. Delaware State Forest (41.266°N, 75.100°W; 275–563 m) and adjoining private lands in Monroe and Pike counties contained a variety of plant community types, including scrub oak forest, dry-oak heath, northern hardwood forest and swamps, glacial bogs, and a conifer swamp (Zimmerman et al. 2012).

Study areas in Tennessee consisted of two mountaintops (708–944 m) that were formerly coal surface mines within the North Cumberland Wildlife Management Area (36.217°N, 84.367°W) in Anderson, Campbell, and Scott counties. One of the study areas was managed on a 2-year rotation with prescribed fire. The predominant land cover was a combination of mixed-mesophytic and oak-hickory forests.

Study areas in West Virginia were eight fenced pastures on and around the Monongahela National Forest in Pocahontas (38.317°N, 80.083°W) and Randolph (38.917°N, 79.733°W) counties. Annual low-intensity grazing and periodic mechanical brush removal maintained early stages of succession within the mixed-mesophytic and northern hardwood forest landscape. Overall, pastures were grassland, forb dominated but featured a gradual transition from grassland to shrubland to forest, especially outside the fenced pasture.

Nest Searching

We located nests by a variety of methods. We mapped the location of territorial males to delineate potential nest-searching areas. We captured and uniquely color banded some of the males using targeted mist netting with playbacks of male songs. Once we located territories of marked individuals, we followed methods similar to Martin and Geupel (1993) to locate nesting activity and identify tagged birds. During nest construction and egg laying and incubation, we found some nests by observing females coming from or going to nests. We also located nests during the nestling stage as males and females made repeated trips to nests with food for the young. Rarely (<10% of the sample), we found nests by systematically searching territories where we had previously observed females or by incidentally locating nests during other field activities. We continued to nest search in territories where females had been observed until a nest was found or until we could no longer find the male or female. We checked nests every three days during laying, incubation, and early nestling stages. We checked nests daily as nestlings came close to their potential fledging date (nestling ages 7–10 days). We searched for nestlings around the nest site when we encountered an empty nest with no signs of predation. We deemed nests successful if we found at least one fledging near the nest site or if there were no signs of predation at the nest. If nests failed, we searched for the renest of an individual female by returning to the failed territory within 1–3 days and observing female nesting behavior as above. We limited potential bias in our sample of nests by using behavioral cues of females to lead us to their nest sites.

Vegetation Characterization

We used a nested plot design (1- and 11.3-m-radius plots) to sample vegetation characteristics at each nest site and a single paired random site. Random sites were 25–50 m from nests and located within a defended territory of a male Golden-winged Warbler. Territories were delineated using a standardized spot mapping technique for all sites and that we presume were available for use as nest sites. At the plot center (for both nest and random paired sites), we visually estimated percent cover to the nearest percent in the field (however, to incorporate potential bias associated with visual estimation we rounded to the nearest 5% for presentation purposes) for forbs, grasses and sedges (hereafter, grass cover), blackberry (*Rubus* spp.), woody vegetation (e.g., tree sprouts), litter, vines, and bare ground within the 1-m-radius plot. We measured litter depth (cm) 1 m from plot center in each cardinal direction. We measured nest height defined as the height from the ground to the rim of the cup (cm). We used a standard collection protocol and trained observers participating in vegetation sampling to reduce potential bias associated with visual estimation methods. In addition, we paired nest plots with random plots and had the same observer(s) on each team conduct the visual estimation of cover for those paired plots.

Following Nudds (1977), we measured visual obstruction from vegetation around each nest and random site using a 2-m-tall density board containing two columns of 10, 20 cm × 20 cm cells. One person stood with the board at plot center while an observer viewed it from 10 m away from each cardinal direction. We recorded the number of cells that were >50% covered with vegetation and calculated vegetation density as the number of cells covered/20 × 100 for an overall percent coverage. Within 11.3 m (0.04 ha) of the plot center, we recorded the number of snags (>10 cm dbh), average shrub height (m), average sapling height (m), and measured the distance from plot center to a mature forest edge. We used a 2.5 m^2/ha basal area prism to measure basal area. The prism defines a variable-width plot around plot center where trees are counted either "in" or "out" of the plot depending on how close they are to plot center and how large they are. The estimate of basal area is calculated by multiplying the number of "in" trees by 2.5 (Avery 1967).

We classified study sites based on their management history because we predicted site history may be important in nest-site selection of Golden-winged Warblers. Sites came from two distinct origins: a site was originally mature forest but then timber harvest or fire led to secondary succession. We classified these study sites as forest derived. Alternatively, a site lacked mature forest characteristics because of past clearing for agriculture, mining, or other land use but was undergoing succession to forest cover. We classified these sites as grassland derived.

Data Analyses

We evaluated characteristics of nest-site selection using spatially matched sets of plots, with each set consisting of a nest plot and an associated random plot. We used only one set of plots per Golden-winged Warbler territory in our analyses. Our habitat data included two distinct types: continuous (vegetation cover, distance to forest edge, etc.; Table 7.1) and categorical (site, region, and forest-derived or grassland-derived type). We were interested in providing habitat management recommendations across the Golden-winged Warbler breeding distribution and conducted analyses for all sites pooled and based on type (forest derived, grassland derived). Given that our data are primarily from the eastern portion

TABLE 7.1
Descriptions of covariates included in a priori *candidate-model sets for evaluating nest-site selection of Golden-winged Warblers in Minnesota, Wisconsin, New York, Pennsylvania, West Virginia, Tennessee, and North Carolina, 2008–2012.*

Covariates	Notation
Linear and additive effects	
Percent bare ground	BG
Percent forb cover	FC
Percent grass cover	GC
Percent *Rubus* cover	RC
Percent vine cover	VC
Percent shrub cover (shrub + *Rubus* + vines)	Shrub
Percent woody cover	WC
Herbaceous cover (grass cover + forb cover)	GC + FC
Curvilinear effects	
Quadratic relationship with vegetation e.g. (grass cover + grass cover ∗ grass cover)	$GC + GC^2$
Cubic relationship with vegetation e.g. (grass cover + grass cover ∗ grass cover + grass cover ∗ grass cover ∗ grass cover)	$GC + GC^2 + GC^3$
Other structural effects	
Vegetation density	VD
Edge distance	ED

of the distribution, our results and management implications are best suited for the Appalachian breeding-distribution segment.

We used conditional logistic regression to compare continuous covariates (see Table 7.1) of Golden-winged Warbler nest-site plots to random plots (Hosmer et al. 2000). We modeled the differences between matched sets (nest and paired random plots) for all sites and years combined. Given that conditional logistic regression evaluates the difference between matched pairs, categorical variables do not perform as well and can result in spurious results (Hosmer et al. 2000). Therefore, for those covariates that were consistent predictors of nest-site selection, we used Simple Saddlepoint Approximation (SSA) (Renshaw 1998, Matis et al. 2003) to graphically evaluate differences among categorical covariates of interest using program R (R Development Core Team 2013). SSA uses the mean, variance, and skewness of variables to find a general saddlepoint approximation of a probability distribution, which is akin to an approximation of the probability density function (pdf). We used SSA to obtain the respective pdf for nest sites and random points. The SSA approach can provide additional perspective about the data structure of specific covariates identified as important, especially when sample sizes are small and distributions are not approximately normal (Demaso et al. 2011). A selection function value of $\int(x) > 1$ indicates selection, or use greater than availability; a value of $\int(x) < 1$ indicates avoidance, or use less than availability; and a selection value of $\int(x) = 1$ indicates no difference in use compared to availability. As such, we interpret random use with respect to an individual vegetation parameter as $\int(x) = 1$. SSA does not allow, however, for explicitly testing for differences in covariates among sites or among Golden-winged Warbler nest plots and random plots. It is difficult to compute analytic error bounds for Simple Saddlepoint Approximations (Smyth and Podlich 2002, Butler 2007). However, we used a bootstrapping approach following Butler and Bronson (2002) and Bronson (2001) to generate 95% confidence bounds, represented as error clouds, to provide a measure of uncertainty for SSAs.

We developed, *a priori*, candidate models for comparisons of vegetation characteristics on nest versus random plots based on factors identified in previously published studies (Klaus and Buehler 2001, Confer et al. 2003, Bullock and Buehler 2008, Aldinger and Wood 2014); these models included additive and factorial combinations of the covariates measured (Table 7.1). We also fit curvilinear models with quadratic and cubic trends to evaluate for possible nonlinear relationships (Table 7.1). We tested hypotheses related to differences in vegetation structure to identify components of vegetation structure unique to forest-derived and grassland-derived sites compared to all sites pooled. We did not include covariates that were highly correlated in analyses (Pearson correlation > 0.7, PROC CORR; SAS Institute 2012). We conducted separate analyses for categorical variables, including site type, forest derived, or grassland derived, to evaluate relative importance of vegetation characteristics among sites with contrasting management origins. In doing so, we could provide habitat management recommendations across the Golden-winged Warbler breeding distribution for all sites pooled and independently based on origin type (forest derived, grassland derived). Furthermore, as noted earlier, categorical variables can result in spurious results in matched-pairs conditional logistic regression (Hosmer et al. 2000). We predicted that nest sites would be associated with a combination of covariates because Golden-winged Warbler nests are typically located in patches of herbaceous vegetation in association with shrubs, saplings, and mature trees (Confer et al. 2011). A primary objective of modeling was to evaluate relative importance of individual predictor variables, and we normalized likelihoods across model subsets within each of our three analyses (sites pooled, forest-derived, and grassland-derived sites) such that Akaike model weights summed to 1 (Burnham and Anderson 2002:167–169, 447–448; Williams et al. 2002:433; Zuur et al. 2009:487).

We conducted conditional logistic regression analyses to model relationships between nest sites and vegetative characteristics using SAS (PROC LOGISTIC; Hosmer et al. 2000, SAS Institute 2012). We ranked competing models using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich et al. 1998). We identified models of interest as those with $\Delta AIC_c \leq 7$ and reported their associated model weights (w_i; Burnham and Anderson 2002). We further described models with $\Delta AIC_c \leq 2$ as those having "substantial empirical support" and we described models with $2 < \Delta AIC_c \leq 7$ as those having "less empirical support" and models with $\Delta AIC_c > 10$

having "no empirical support" (Burnham and Anderson 2002:70). We also calculated and evaluated profile likelihood 95% confidence intervals (CI) around parameter estimates for those models with substantial empirical support (Venzon and Moolgavkar 1988) and considered CIs not containing zero as evidence for statistical significance. We reported mean values for individual parameter differences between nest and random plots, and 95% CIs around those differences and used log-odds ratios to indicate statistical significance. Descriptors of vegetation are more useful to land managers than mean values for individual parameters differences between nest and random sites and, as such, we also report selection values from SSA for specific nest-site variables based on continuous selection functions (Jensen 1995). We present the SSA analysis for all sites pooled and then stratified the analysis further into site type (forest derived, grassland derived). We report means, precision estimates (CIs), and log-odds ratios to evaluate the selection of individual vegetation characteristics for successful nests compared to failed nests.

RESULTS

We analyzed nest-site characteristics of Golden-winged Warbler nests and associated random sites using 442 paired plots. Sample sizes of nests in landscapes categorized as grassland derived (n = 219; North Carolina, West Virginia, and Tennessee) and forest derived (n = 223; Minnesota, New York, Pennsylvania, and Wisconsin) were similar. If information for nests was incomplete those vegetation data were excluded from analyses (<1% of all nest data).

Nest-Site Characteristics

Nests were typically located on or near the ground. The average height to nest rim for nests across all sites was 12 cm (±0.3 SE), 11 cm (±0.5 SE) for forest-derived sites, and 13 cm (±0.3 SE) for grassland-derived sites.

We evaluated 44 candidate models (20 linear or additive, 12 curvilinear, and 12 habitat-structure models) at all sites pooled, and forest-derived and grassland-derived sites; however, we only report those models with $\Delta AIC_c < 7.0$. For all sites pooled, two linear or additive models received substantial empirical support ($\Delta AIC_c < 2.0$; Table 7.2) indicating that bare ground cover, grass cover, forb cover, woody cover, and blackberry may be important vegetation characteristics associated with nest sites of Golden-winged Warblers. The two models with substantial support for all sites pooled carried >93% of the overall model weight (Table 7.2). SSA suggested that Golden-winged Warbler nests were associated with limited bare ground (0%–10% cover; Figure 7.2) and the model including bare ground was 2.3 times more likely than the next best model without bare ground. SSA also revealed that Golden-winged Warbler nests were more commonly associated with grass cover <55% (Figure 7.3) and woody cover within the range of 15%–35% (Figure 7.3). A third model including vine cover received less empirical support ($\Delta AIC_c = 4.53$; Table 7.2) and had a relatively low model weight ($w_i = 0.067$; Table 7.2). Golden-winged Warbler habitat selection for nests located at forest-derived sites was similar to the pooled sites with the exception that vine cover was less important ($w_i = 0.010$; Table 7.3). In contrast, the two models with substantial support for nests at grassland-derived sites both included vine cover and comprised >0.99 of the overall model weight (Table 7.3). The only models receiving substantial empirical support that included curvilinear covariates included bare ground (cubic and quadratic terms) for all sites pooled (Table 7.2) and bare ground (cubic and quadratic terms) for grassland-derived sites (Table 7.4). In addition, models for all sites pooled with grass cover (cubic term), and *Rubus* cover (cubic and quadratic terms) received less empirical support ($\Delta AIC_c < 7.0$; Table 7.2), and models for grassland-derived sites with *Rubus* cover (cubic and quadratic terms) also received less empirical support ($\Delta AIC_c < 7.0$; Table 7.4). In forest-derived sites, the model that included grass cover was overwhelmingly the most empirically supported model and received >0.99 of the overall model weight (Table 7.3). Based on SSA, Golden-winged Warbler nests at forest-derived sites were associated with 10%–65% grass cover (Figure 7.3).

The most important covariates in models for all sites pooled were bare ground cover and grass cover ($\Sigma w_i = 0.69$ and 0.45, respectively; Table 7.5). The most important covariate in models of forest-derived sites was grass cover ($\Sigma w_i = 0.80$; Table 7.5). The most important covariates in models of grassland-derived sites were bare ground cover,

TABLE 7.2

Empirically supported models ($\Delta AIC_c < 7$) of nest-site selection, all sites in all states, included in conditional logistic regression analyses comparing characteristics of Golden-winged Warbler nests and paired randomly sampled sites in Minnesota, Wisconsin, New York, Pennsylvania, West Virginia, Tennessee, and North Carolina, 2008–2012.

Model[a]	K	Deviance	AIC_c	ΔAIC_c	w_i
Linear and additive cover effects					
BC + GC + FC + WC + RB	5	−1063.412	543.706	0.000	0.644
GC + FC + WC + RB	4	−1070.610	545.305	1.599	0.289
GC + FC + WC + RB + VC	5	−1096.478	548.239	4.533	0.067
Curvilinear cover-type effects					
$BC + BC^2 + BC^3$	3	−1168.354	590.177	0.000	0.433
$BC + BC^2$	2	−1173.172	590.586	0.409	0.353
$GC + GC^2 + GC^3$	3	−1173.616	592.808	2.631	0.116
$RC + RC^2$	2	−1176.634	594.317	4.140	0.055
$RC + RC^2 + RC^3$	3	−1179.074	595.537	5.360	0.030
Structural cover-type effects					
$VD + VD^2 + VD^3$	3	−993.370	502.685	0.000	0.973

[a] Covariate notation described in Table 7.1.

Rubus cover, vine cover, and forb cover ($\sum w_i = 0.46$, 0.46, 0.40, 0.41, respectively; Table 7.5).

For all sites pooled, nest sites (within the 1-m plot) contained less bare ground compared to random sites within the territory (Table 7.6); this result was similar for nests on forest-derived sites and grassland-derived sites (Table 7.6). Nest sites had greater woody cover than what was present at random sites within the territory for all sites pooled, forest-derived sites, and grassland-derived sites (Table 7.6). In addition, grass cover was much greater at nest sites compared to random sites within the territory for nests located at forest-derived sites (Table 7.6). At grassland-derived sites, however, there was less grass cover at nest sites than that present at random sites within the territory. Blackberry cover, but not forb cover was greater at nest sites compared to that present at random sites within the territory on grassland-derived sites (Table 7.6).

Nest Habitat Structure

Models of habitat structure associated with nests that received substantial empirical support included cubic relationships with vegetation density for all sites pooled ($w_i = 0.973$; Table 7.2) and cubic and quadratic relationships with vegetation density within forest-derived sites ($\sum w_i = 0.950$; Table 7.3). At grassland-derived sites, vegetation density appeared to be an important covariate ($w_i = 0.450$ for models containing vegetation density with $\Delta AIC_c < 2.0$; Table 7.4), but shrub cover appeared to be more strongly associated with nest sites (WC + VC + RC; $w_i = 0.550$ with $\Delta AIC_c < 2.0$; Table 7.4). Based on SSA, Golden-winged Warblers selected nest sites with vegetation density ranging from 10% to 35% (Figure 7.3).

Vegetation Characteristics and Nest Success

Successful nests of Golden-winged Warblers at forest-derived sites had greater grass cover compared to unsuccessful nests (Table 7.7), whereas successful nests located at grassland-derived sites had similar amounts of grass cover compared to unsuccessful nests (Table 7.7). No other covariates differed between successful and unsuccessful nests (Table 7.7).

DISCUSSION

Our objective was to identify habitat characteristics associated with nest sites across a broad geographic scale to guide habitat management for breeding Golden-winged Warblers. We hypothesized that

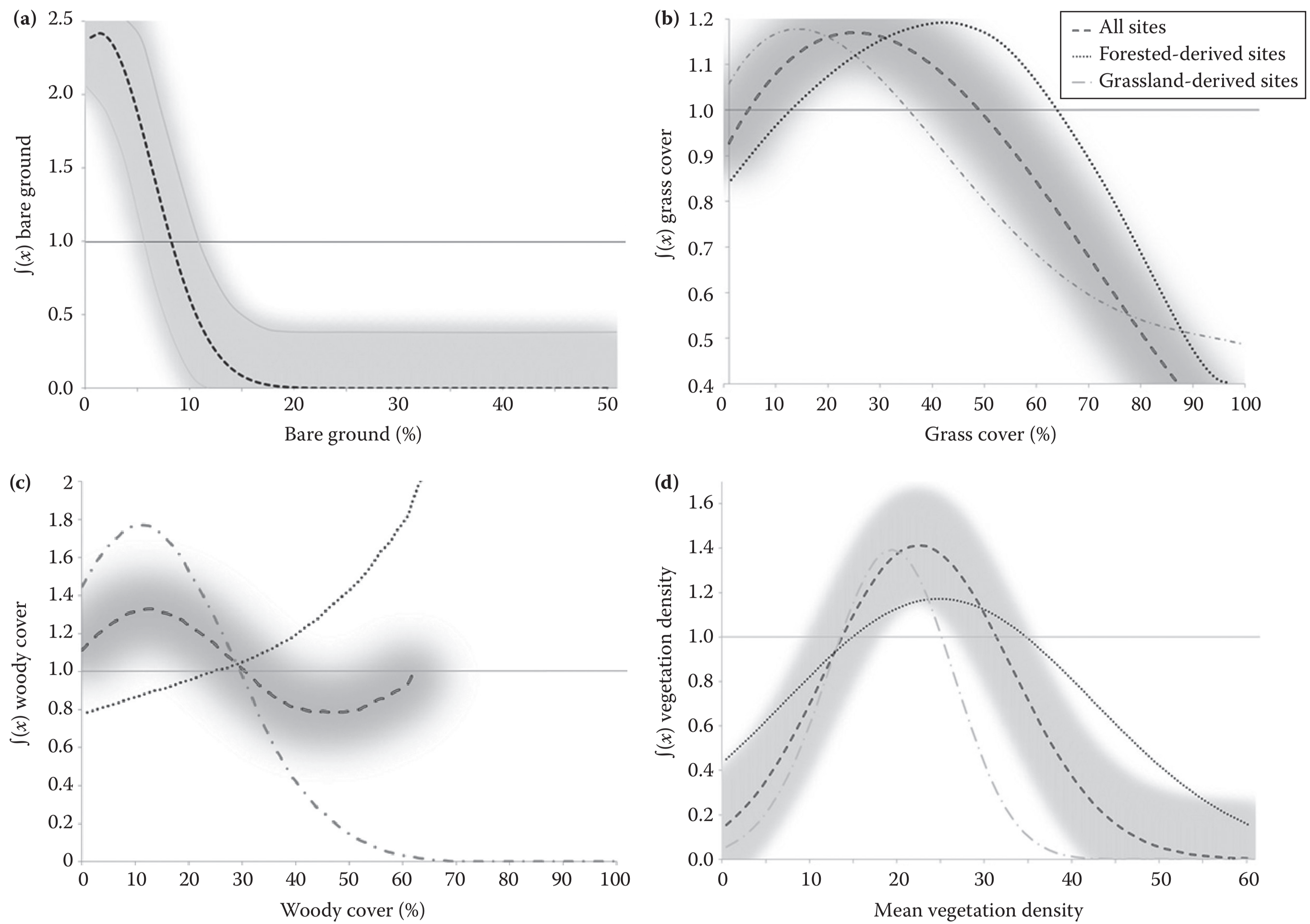

Figure 7.2. Selection function based on SSAs for (a) bare ground cover; (b) grass cover; (c) woody cover; and (d) vegetation density at Golden-winged Warbler nests in Minnesota, New York, North Carolina, Pennsylvania, Tennessee, West Virginia, and Wisconsin for all sites pooled, 2008–2012. Gray-shaded region reflects the 95% bootstrapped confidence limits.

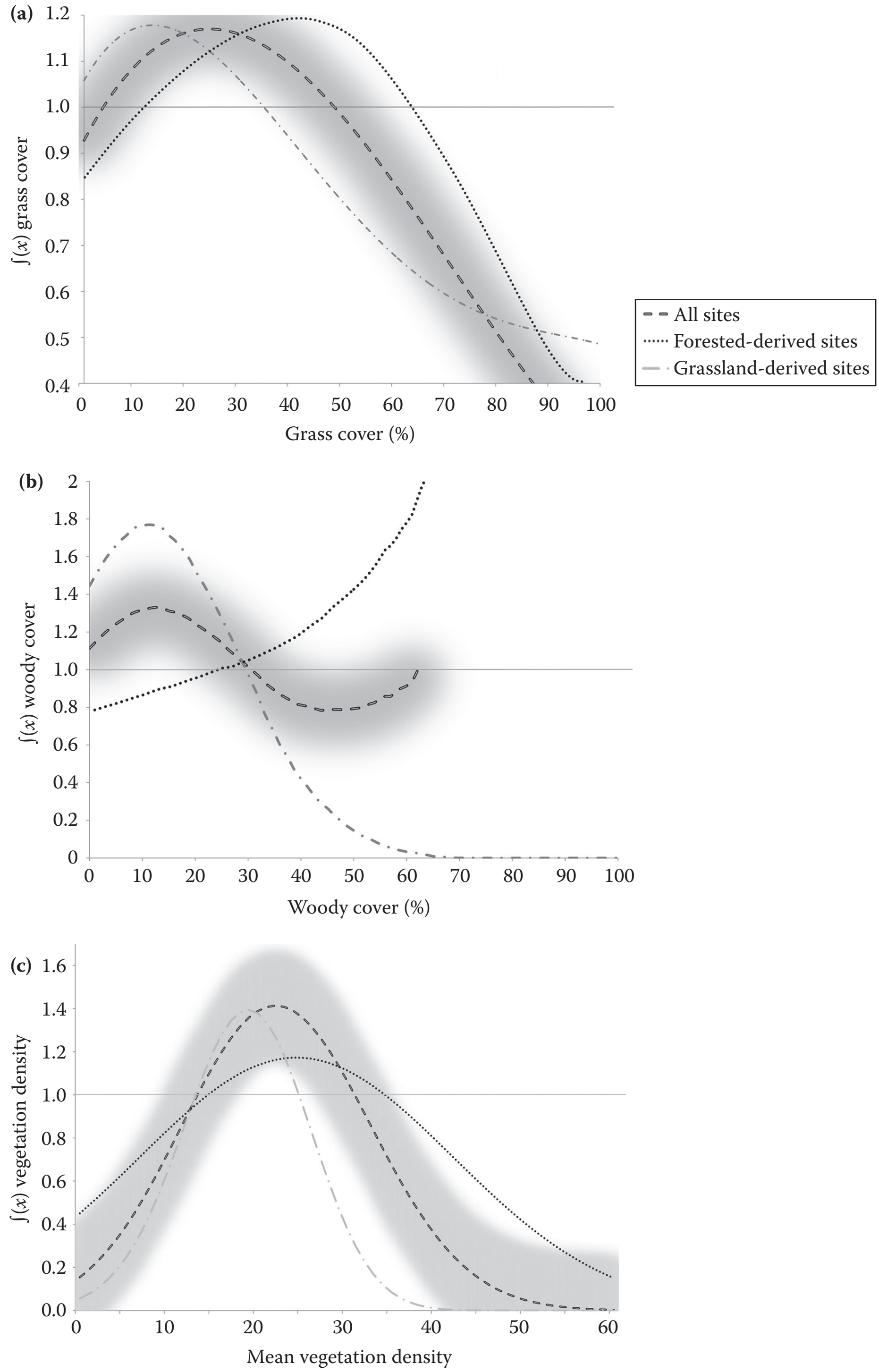

Figure 7.3. Selection function based on SSAs for (a) grass cover; (b) woody cover; and (c) vegetation density at Golden-winged Warbler nests in Minnesota, New York, North Carolina, Pennsylvania, Tennessee, West Virginia, and Wisconsin delineated by all sites, forest-derived sites and grassland-derived sites, 2008–2012. Gray-shaded region reflects the 95% bootstrapped confidence limits.

TABLE 7.3

Empirically supported models ($\Delta AIC_c < 7$) of nest-site selection, in forest-derived sites, in conditional logistic regression analyses comparing characteristics of Golden-winged Warbler nests and paired randomly sampled sites in Minnesota, Wisconsin, New York, Pennsylvania, West Virginia, Tennessee, and North Carolina, 2008–2012.

Model[a]	K	Deviance	AIC_c	ΔAIC_c	w_i
Linear and additive cover effects					
BC + GC + FC + WC + RB	5	−509.84	266.92	0.00	0.98
Curvilinear cover-type effects					
$GC + GC^2 + GC^3$	3	−554.41	283.20	0.00	0.61
$GC + GC^2$	2	−560.13	284.07	0.86	0.39
Structural cover-type effects					
$VD + VD^2 + VD^3$	3	−450.47	231.23	0.00	0.62
$VD + VD^2$	2	−456.97	232.48	1.25	0.33
VD	1	−468.51	236.25	5.02	0.05

[a] Covariate notation described in Table 7.1.

TABLE 7.4

Empirically supported models ($\Delta AIC_c < 7$) of nest-site selection, in grassland-derived sites, in conditional logistic regression analyses comparing characteristics of Golden-winged Warbler nests and paired randomly sampled sites in Minnesota, Wisconsin, New York, Pennsylvania, West Virginia, Tennessee, and North Carolina, 2008–2012.

Model[a]	K	Deviance	AIC_c	ΔAIC_c	w_i
Linear and additive cover effects					
GC + FC + WC + VC + RB	5	−470.92	245.46	0.00	0.72
BC + GC + FC + WC + VC + RB	6	−470.68	247.34	1.88	0.28
Curvilinear cover-type effects					
$BG + BG^2 + BG^3$	3	−575.52	293.76	0.00	0.48
$BG + BG^2$	2	−580.34	294.17	0.41	0.39
$RC + RC^2$	2	−586.00	297.00	3.24	0.09
Structural cover-type effects					
$Shrub + shrub^2$	2	−541.97	274.99	0.00	0.39
$VD + VD^2$	2	−544.06	276.03	1.04	0.23
$VD + VD^2 + VD^3$	3	−540.31	276.16	1.17	0.22
$Shrub + shrub^2 + shrub^3$	3	−541.56	276.78	1.80	0.16

[a] Covariate notation described in Table 7.1.

in spite of the variety of cover types that Golden-winged Warblers occupied in our study areas, we would be able to identify some characteristics consistently associated with nest sites. Ultimately, we speculated that these characteristics may be linked to increased nest survival (Aldinger et al. 2015). Until this study, no habitat selection studies have been conducted across a broad geographic scale for breeding Golden-winged Warblers. Boves et al. (2013), however, in a recent regional study on Cerulean Warbler (*Setophaga cerulea*) breeding habitat selection, demonstrated that habitat

TABLE 7.5
Cumulative Akaike weights for covariates included in the empirically supported models assessing vegetation characteristics of nest-site selection for Golden-winged Warblers, 2008–2012.

	All sites	Forest-derived sites	Grassland-derived sites
Cover type	Σw_i	Σw_i	Σw_i
Bare ground	0.69	0.39	0.46
Grass cover	0.45	0.80	0.19
Forb cover	0.40	0.40	0.45
Rubus cover	0.43	0.40	0.46
Woody cover	0.40	0.41	0.40
Vine cover	0.03	0.00	0.41

We summed Akaike weights, Σw_i, from individual candidate models with $\Delta AIC_c < 2$ containing each covariate of interest.

selection varied among study sites at the territory scale, although nest-site selection was consistent within Appalachian region sites. If habitat selection in birds is largely driven by local, site-specific conditions, then developing management guidelines for broad geographic areas will be problematic (McNew et al. 2013). Developing management guidelines based on studies of habitat selection without linking the habitat characteristics to nest success and postfledging survival further reduces the likelihood for successful conservation strategies (Jones 2001).

We identified several habitat characteristics that were associated with nest sites across all sites pooled and within subsets of sites based on their origin (forest derived or grassland derived) using visual assessment of vegetation. Several studies have compared methods estimating vegetation cover with varying results among the literature whereby some have suggested that visual estimation produces unreliable results within (Kennedy and Addison 1987) or among differing methods (Symstad et al. 2008). Although other studies suggest that visual estimation is reliable and accurate when conducted by trained observers and when establishing discrete categories (Kercher et al. 2003, Symstad et al. 2008). We recognize that cover estimates and associated precision may be potentially biased in our study due to observer subjectivity. However, the same observers estimated cover on paired sites; hence, comparison of vegetation at random points and nest sites are valid for assessing differences in cover types with respect to nest-site selection. As such, despite inherent uncertainty around point estimates for individual cover types, general trends about and evaluation of differences in cover type are germane to understanding the biological importance of nest-site selection in the context of site origin.

Nest sites in our study were most strongly associated with low amounts of bare ground (Figure 7.2), and intermediate amounts of grass cover (Figure 7.3a), woody cover (Figure 7.3b), and vegetation density (Figure 7.3c). The nature of the relationships varied depending on whether the site originated from mature forest and was undergoing secondary succession after timber harvest or fire, or whether the site originated from farmland or mining and was undergoing primary succession to forest cover. Furthermore, we observed that Golden-winged Warblers selected for grass cover that was deficient at forest-derived sites, and woody cover is a structural vegetation component that may be linked to nest survival (Aldinger et al. 2015). Selection at the nest-site level may be linked to the landscape context of vegetation at a site and is an ecological phenomenon that has received growing recognition as being of critical importance for understanding the dynamics of natural systems (Borcard and Legendre 2002, Lichstein et al. 2007). Recent studies suggest that incorporating vegetation metrics and spatial habitat context may improve inference from ecological models and help guide on-the-ground management (Thogmartin et al. 2004, Thogmartin and Knutson 2007, van Teeffelen and Ovaskainen 2007). Thus, our results provide

TABLE 7.6

Percent cover of vegetation for Golden-winged Warbler nests (n = 412) compared to paired-random sites in Minnesota (n = 18), New York (n =78), North Carolina (n = 8), Pennsylvania (n = 101), Tennessee (n = 129), West Virginia (n = 96), and Wisconsin (n = 40) delineated by type (forest derived, grassland derived, and all sites pooled), 2008–2012.

	Nest site			Paired random site			
	Mean	SE	95% CI	Mean	SE	95% CI	Selection
All sites							
Bare ground	1	0.1	(0, 1)	4	0.5	(3, 5)	
Grass cover	21	0.9	(19, 23)	20	1.0	(17, 22)	
Forb cover	38	1.3	(35, 40)	34	1.3	(32, 37)	
Rubus cover	11	0.8	(10, 13)	10	0.9	(8, 12)	
Woody cover	18	1.0	(15, 20)	12	0.9	(10, 14)	+
Vine cover	3	0.4	(2, 3)	3	0.4	(2, 3)	
Forest-derived sites							
Bare ground	1	0.3	(1, 2)	5	0.8	(3, 6)	
Grass cover	21	1.2	(18, 23)	16	1.4	(13, 18)	+
Forb cover	27	1.7	(24, 31)	26	1.7	(23, 29)	
Rubus cover	8	1.1	(5, 10)	8	1.2	(5, 10)	
Woody cover	26	1.7	(23, 29)	19	1.6	(16, 22)	+
Vine cover	2	0.5	(1, 3)	2	0.5	(1, 3)	
Grassland-derived sites							
Bare ground	1	0.2	(0, 1)	3	0.6	(2, 4)	
Grass cover	22	1.1	(19, 24)	24	1.5	(21, 26)	
Forb cover	48	1.5	(45, 51)	42	1.7	(39, 45)	
Rubus cover	15	1.2	(13, 17)	12	1.4	(9, 15)	
Woody cover	9	1.0	(7, 11)	6	0.7	(4, 7)	+
Vine cover	3	0.6	(2, 4)	4	0.7	(2, 5)	

We report standard error (SE) and derived 95% CI; we indicate selection greater than (+) and less than (−) observed at random locations for only those covariates whose CIs are not overlapping.

some of the first empirical evidence that nest-site selection may vary depending on site origin. As such, these selective cues may prove important for understanding how habitat characteristics influence behavioral decisions during nest-site selection, which may depend upon the local environment experienced by breeding females.

Breeding Golden-winged Warblers require diverse vegetation composition comprising herbaceous and woody cover types that create patches of potential nest sites within a larger forested landscape. The strongest patterns of selection among sites we studied were related to amount of herbaceous cover (Figure 7.3) and vegetation density (Figure 7.3). In sites of mature forest origins, woody cover generally dominated the site but herbaceous cover was less abundant. Nest-site selection on these sites was associated with greater herbaceous cover (Figure 7.3). In contrast, on sites with grassland-derived origins, herbaceous cover was dominant, with lower availability of woody cover. Nest-site selection on these sites was associated with small amount of herbaceous cover. Selection of woody cover on all sites may be a result of different forms of vegetation providing similar structural elements, including shrubs, saplings, and blackberry cover. Selection for physical visual obstruction at nest sites, in general, was similar among all sites, based on our measures of vegetation density (Figure 7.3), but it is evident

TABLE 7.7

Percent cover (%) of vegetation of Golden-winged Warbler successful (n = 221) and failed nests (n = 171) in Minnesota (n = 18), New York (n = 98), North Carolina (n = 8), Pennsylvania (n = 101), Tennessee (n = 129), West Virginia (n = 96), and Wisconsin (n = 40), 2008–2012.

	Nest successful				Nest failed				
	N	Mean	SE	95% CI	N	Mean	SE	95% CI	Selection
All sites									
Bare ground	221	1	0.2	(1, 2)	171	1	0.3	(1, 2)	
Grass cover	221	23	1.2	(21, 25)	171	19	1.5	(16, 22)	
Forb cover	221	37	1.9	(34, 41)	171	40	2.0	(36, 44)	
Rubus cover	221	11	1.2	(8, 13)	171	13	1.4	(10, 16)	
Woody cover	221	16	1.4	(13, 19)	171	16	1.8	(13, 20)	
Vine cover	221	2	0.4	(1, 3)	171	4	0.8	(2, 5)	
Forest-derived sites									
Bare ground	115	2	0.4	(1, 2)	73	2	0.5	(1, 3)	
Grass cover	115	25	1.9	(21, 29)	73	14	2.2	(10, 18)	+
Forb cover	115	27	2.7	(22, 33)	73	28	3.1	(22, 34)	
Rubus cover	115	8	1.4	(5, 10)	73	8	2.2	(4, 13)	
Woody cover	115	22	2.2	(17, 26)	73	28	3.4	(21, 34)	–
Vine cover	115	1	0.4	(0, 2)	73	4	1.2	(2, 6)	–
Grassland-derived sites									
Bare ground	106	1	0.2	(0, 1)	98	1	0.3	(0, 1)	
Grass cover	106	21	1.5	(17, 24)	98	23	1.9	(18, 26)	
Forb cover	106	48	2.3	(44, 52)	98	48	2.3	(44, 53)	
Rubus cover	106	14	2.0	(10, 18)	98	16	1.7	(13, 19)	
Woody cover	106	10	1.4	(8, 13)	98	8	1.5	(5, 11)	
Vine cover	106	2	0.7	(1, 4)	98	4	1.2	(1, 6)	

We report standard error (SE) and derived 95% CI. We indicate selection greater than (+) and less than (−) observed at random locations for only those covariates whose CIs are not overlapping.

that there is a threshold at which vegetation can be too dense or not dense enough for nesting.

Birds are thought to select breeding habitat in a hierarchical fashion, with first-order selection defining the breeding distribution of a species (Johnson 1980). Second-order selection defines the home range of an individual. Third-order selection by males defines the breeding territory, presumably to attract a female by offering potential suitable nest sites and enabling successful postfledging survival (Streby et al. 2014; Chapter 8, this volume). Females are then constrained within the territories established by males to what is available for nest-site selection and postfledgling habitat. Our study demonstrates that nest-site selection is not random within the territory, but instead is driven by certain vegetation components, presumably because they enhance nest survival (Aldinger et al. 2015) and potentially subsequent fledgling survival (Streby et al. 2014). It is apparent that females are selecting for a variety of conditions to optimize their nest sites to the local environment based on habitat availability or other limitations. Thus, recognizing these habitat limitations in the context of site origin and managing to match habitat selection at the territory level is critical to ensure adequate nesting cover.

CONSERVATION IMPLICATIONS

We documented Golden-winged Warbler nest-site characteristics across a broad geographic scale to help guide management of nesting habitat. As a result of the development of the Golden-winged Warbler Conservation Action Plan (A. M. Roth et al., unpubl. plan) and other associated research, it has become apparent that the Appalachian and Great Lakes regions support disjoint breeding-distribution segments (Chapter 1, this volume) and should be treated as distinct conservation management units. Therefore, the habitat characteristics that we measured and the saddlepoints in the SSA plots can be used as general conservation targets by managers as they improve forest-derived or grassland-derived cover types for Golden-winged Warblers, but our results are likely more relevant to the Appalachian breeding-distribution segment than the Great Lakes breeding-distribution segment. Our results suggest that nest-site selection occurs within the following cover-type ranges: 0%–10% bare ground, 40%–80% herbaceous (forb cover + grass cover), and 15%–35% shrub cover (woody cover + *Rubus* cover + vine cover). However, depending on the origin of the site as forest-derived or grassland-derived, the upper or lower ranges for these covariates may vary slightly due to vegetation sampling error. In particular among forest-derived sites, it may be necessary to manage for adequate amounts of grass cover. As with management of any ephemeral resource, management of nest habitat for Golden-winged Warblers must address the continual process of forest succession, as sites grow into suitable condition postdisturbance but then mature beyond suitable condition. A continual need for management in some cover types in part explains the challenge to develop successful conservation strategies for Golden-winged Warblers. Incorporating nesting habitat requirements with postfledging habitat requirements within managed landscapes adds another layer of management complexity (Streby et al. 2014; Chapter 8, this volume).

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