



## FACTORS INFLUENCING GOLDEN-WINGED WARBLER (*VERMIVORA CHRYSOPTERA*) NEST-SITE SELECTION AND NEST SURVIVAL IN THE CUMBERLAND MOUNTAINS OF TENNESSEE

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**ABSTRACT.**—Studies of reproduction and habitat use are essential for any species assessment, especially for species with declining populations. We compared habitat in nest sites and randomly selected sites within Golden-winged Warbler (*Vermivora chrysoptera*) territories. We also modeled the effects of temporal and biotic factors on daily nest survival in relation to the constant-survival model. The percent cover of herbaceous vegetation was greater at nest sites, and that of woody vegetation was greater at non-nest sites. There was support for models with annual variation and a decline in nest survival throughout the nesting season, but the constant-survival model performed equally well. One parameter performed marginally better than the constant-survival model: nests with a woody stem in the substrate had lower nest-survival rates. We conclude that nest-site selection was nonrandom, such that females use specific criteria to select nest sites. However, habitat characteristics did not appear to significantly affect daily nest survival or, therefore, predation rates. Until factors that affect predation rates are better understood, conservation strategies that increase breeding habitat with specific nest-site features may be more successful than attempts to directly control nest survival. *Received 11 May 2007, accepted 10 October 2007.*

**Key words:** Cumberland Mountains, daily nest survival, early successional, Golden-winged Warbler, nest-site selection, program MARK, *Vermivora chrysoptera*.

### **Factores que Influencian la Selección de Sitios de Anidación y la Supervivencia de los Nidos en *Vermivora chrysoptera* en las Montañas Cumberland, Tennessee**

**RESUMEN.**—Los estudios de la reproducción y el uso de hábitat son esenciales para cualquier evaluación de poblaciones de una especie, especialmente para aquellas que presentan poblaciones en declive. Comparamos el hábitat de los sitios de anidación y de sitios seleccionados al azar dentro de territorios de *Vermivora chrysoptera*. También modelamos los efectos de factores temporales y bióticos sobre la supervivencia diaria de los nidos, en relación con el modelo de supervivencia constante. El porcentaje de cobertura de vegetación herbácea fue mayor en los sitios de anidación, y el de vegetación leñosa fue mayor en los sitios donde no había nidos. Los modelos avalados presentaron variación anual y un declive en la supervivencia de los nidos a lo largo de la época de anidación, pero el modelo de supervivencia constante se desempeñó igualmente bien. Un parámetro se desempeñó marginalmente mejor que el modelo de supervivencia constante: los nidos con un tallo leñoso en el sustrato presentaron tasas de supervivencia menores. Concluimos que la selección de sitios de anidación no fue azarosa, de modo que las hembras usan criterios específicos para escoger los sitios donde anidan. Sin embargo, las características del hábitat no parecieron afectar significativamente la supervivencia diaria de los nidos ni, por lo tanto, las tasas de depredación. Hasta que los factores que afectan las tasas de depredación sean mejor entendidos, las estrategias de conservación que incrementan la calidad del hábitat de reproducción con características específicas de los sitios de anidación podrían ser más exitosas que los intentos para controlar directamente la supervivencia de los nidos.

STUDIES OF REPRODUCTION and habitat use are particularly important for species experiencing significant population declines. However, because it is difficult to collect these data, management recommendations for declining species are often based solely on species occurrences or population densities (Van Horne 1983, Scott et al. 2002). Assessing habitat use versus availability

is more informative than comparing used with unused habitat (Johnson 1980, Jones 2001), because, in addition to the expected avoidance of some environmental factors, biological factors such as competition, predation, and density can lead to non-use (Rotenberry and Wiens 1980, Haila et al. 1996). When productivity data are available for avian species, only apparent-nest-success

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estimates or Mayfield nest-survival estimates (Mayfield 1961), which assume constant survival over time, are typically provided. Only recently have analytical methods become available that allow daily nest survival to vary with time and as a function of biologically meaningful covariates (Dinsmore et al. 2002, Shaffer 2004). As a result, researchers can gain a better understanding of the factors that influence daily-nest-survival rates (DSR) to answer questions about variation within a region or across habitats and to make more informed management decisions.

The Golden-winged Warbler (*Vermivora chrysoptera*) is a Nearctic–Neotropical migratory songbird that requires early-successional breeding habitat. Golden-winged Warblers nest on the ground in areas with scattered trees and shrubs and an herbaceous understory of grasses and forbs found in either upland or wetland settings (Confer 1992). Populations of Golden-winged Warblers are declining throughout the species' range as early-successional habitats revert to mature forest and as upland and wetland habitats are lost to human development (Confer 1992, Buehler et al. 2007). These population declines are leading to extirpation of the species from areas that have supported Golden-winged Warblers for the past several centuries (i.e., Georgia, South Carolina, Virginia, Massachusetts, Connecticut, Rhode Island, Vermont, New Hampshire, Indiana, Illinois, and Ohio; Buehler et al. 2007). The range expansion of the Blue-winged Warbler (*Vermivora pinus*) and resulting hybridization may also be contributing to population declines in Golden-winged Warblers (Gill 1997, Vallender et al. 2007). This phenomenon is occurring range-wide and is currently a major problem in the northeastern United States. Breeding Bird Survey (BBS) data indicate that populations have declined an average of 2.5% per year survey-wide ( $P < 0.001$ ;  $n = 274$  routes) over the past 40 years of monitoring (1966–2005; Sauer et al. 2005). Consequently, the Golden-winged Warbler is considered a high-priority species for conservation by Partners in Flight and the U.S. Fish and Wildlife Service.

Published data on the Golden-winged Warbler's breeding biology are rare. Confer et al. (2003) demonstrated that herb and shrub cover were positively correlated with clutch size in Golden-winged Warblers, increased tree cover was positively correlated with number of fledglings, and herbaceous cover was correlated with more Brown-headed Cowbird (*Molothrus ater*) eggs. Klaus and Buehler (2001) showed that nest sites had fewer saplings and less canopy cover than randomly selected sites within a territory. Although this information is useful, no studies have used rigorous statistical methods to assess whether DSR of Golden-winged Warblers vary with time or with other biologically meaningful covariates.

The Cumberland Mountains population of Golden-winged Warblers deserves conservation attention for several reasons. Most published studies of nesting and habitat use were conducted where habitats greatly differ from the Cumberland Mountains. Most Golden-winged Warblers in the Cumberlands occupy coal surface mines that were reclaimed 15–30 years ago. With the resurgence of mining in the region, there is interest in reclamation strategies that provide high-quality early-successional habitats for priority species such as the Golden-winged Warbler. Furthermore, little hybridization is likely occurring in the Cumberlands, because of elevational separation of Golden-winged and Blue-winged warblers (but see Vallender et al. 2007), such that loss of

habitat, nest predation, or both may be limiting factors in this region. Phenotypic hybrid individuals constitute <10% of the studied Cumberland Mountains population. Finally, the potential for management is great for this population, considering the large amount of state-owned land and the intact nature of the forests. The current proportion of early- and late-successional habitats in the Cumberlands may mimic natural disturbance at the landscape scale while still maintaining large core areas of mature forests. Indeed, the Cumberland Mountains region is >70% forested (Bulluck 2007). Such a distribution of successional habitat may provide highly productive nesting sites compared with disturbed areas in a more developed–agricultural landscape that may experience more nest predation and parasitism because of edge effects (Rodewald 2002).

The objectives of our research were to (1) compare habitat attributes associated with nest sites to attributes in sites sampled randomly within Golden-winged Warbler territories and (2) determine whether there is a relationship between daily nest survival and year-, date-, nest age-, climate-, and habitat-specific covariates. Increased understanding of factors influencing nest-site selection and nest survival in Golden-winged Warblers is imperative if breeding-season management efforts are to be successful.

## METHODS

**Study area.**—The Cumberland Mountains in northeastern Tennessee extend south from the central Appalachian Mountains in Kentucky, West Virginia, and Pennsylvania. The mean elevation is 580 m, and the highest ridges reach 1,075 m. More than 50,500 ha of this landscape are publicly owned by the Tennessee Wildlife Resources Agency (TWRA); our study sites are located within and adjacent to the Sundquist Forest Wildlife Management Area (Fig. 1). The predominant land-cover of the region is mixed mesophytic forest; ~15% is in early succession because of the surface mining of coal and timber harvests (Bulluck 2007). The Cumberland Mountains are located near the southern extreme of the Golden-winged Warbler's range. In this region, Golden-winged Warblers primarily occupy reclaimed coal surface-mines ( $\geq 10$  years post-reclamation); they also ephemerally occupy sites associated with timber harvests (5–15 years postharvest), at lower densities (Welton 2003, L. Bulluck pers. obs.).

We conducted the study on four coal surface-mines reclaimed in ~1980 ( $n = 2$ ) and ~1990 ( $n = 2$ ) (Table 1). Mine reclamation involved planting Black Locust (*Robinia pseudoacacia*) saplings and a thick herbaceous layer of grasses and forbs to prevent soil erosion. Since reclamation, maples (*Acer* spp.), Yellow Poplar (*Liriodendron tulipifera*), oaks (*Quercus* spp.), and thickets of blackberry (*Rubus* spp.) have become established. Periodic fires (mostly deliberate arson) have maintained the thick herbaceous cover and created numerous snags in all sites. All study sites were at approximately the same elevation (mean = 850 m, range = 770–950 m). We selected these sites because they have relatively high concentrations of breeding Golden-winged Warbler pairs per site, which allowed us to efficiently focus our daily nest searching and monitoring efforts.

**Field methods.**—From 20 April to 30 June 2004–2006, we visited each site every two or three days from sunrise (~0600 hours EST) to midafternoon (~1400 hours). We spent the early morning

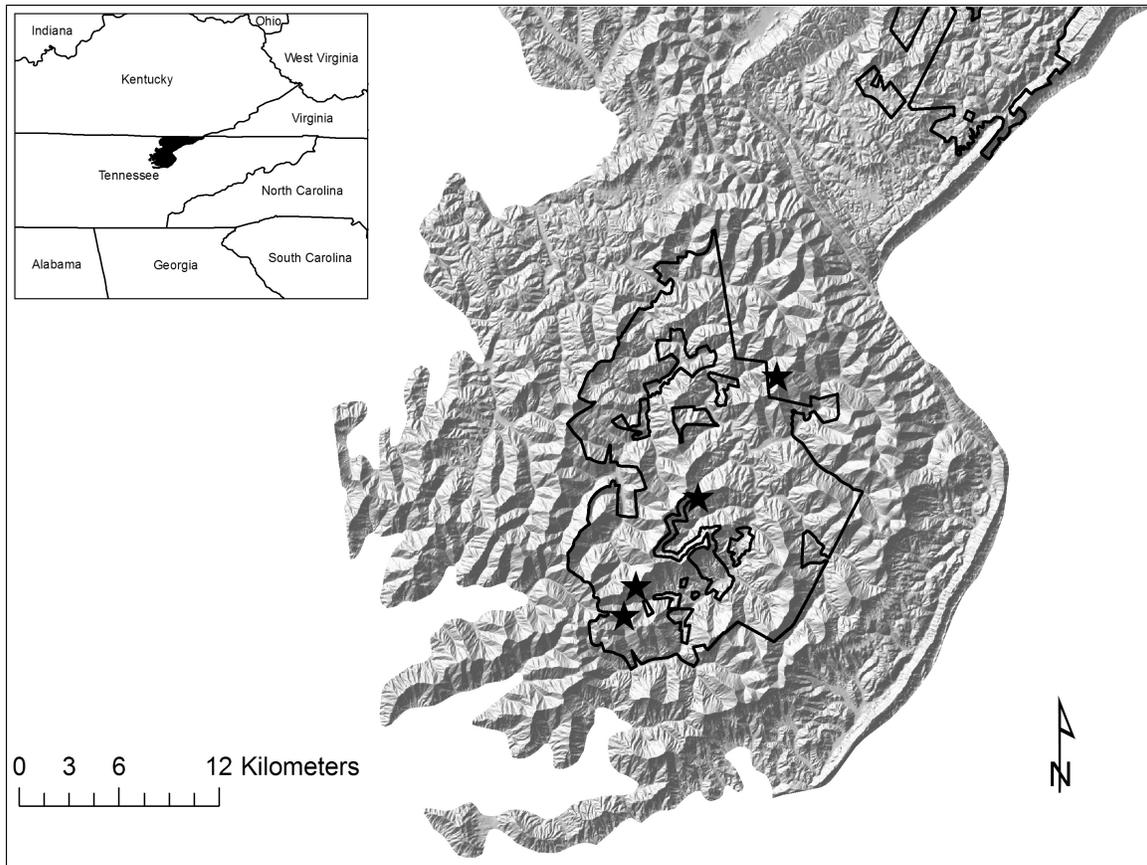


FIG. 1. The Cumberland Mountains ecoregion in northeastern Tennessee and the boundary of the Sundquist Forest Wildlife Management Area. The locations of the four study sites are indicated with stars.

hours (until 1000 hours) observing behavior, mapping territories, and locating nests. To map territories, we followed individually color-marked males during one 30-min visitation period per day and marked their location every 3 min for a total of 10 potential locations per day. We mapped each male’s territory over five visits from 1 May to 15 June, and at least once early and once late in the morning to ensure that we accounted for variation in behavior throughout the morning. Our goal was to collect 40–50 locations

for each male across the breeding season. We marked points using flagging tape and a Trimble GeoExplorer XM GPS unit. We collected vegetation data in an 11.3-m-radius plot (0.04 ha) around each nest as well as at three randomly selected locations within the territory. These data were collected in early to mid-June (average nest-vegetation sampling date = 18 June), soon after all nests were complete (average fledge–fail date = 30 May). We recognize that the vegetation height and density may have changed slightly during this ~2.5-week interim between nest completion and vegetation sampling, but the change was not likely significant. Three non-nest vegetation plots per mapped territory were randomly selected using a random-point generator extension (Jenness 2005) in ARCVIEW, version 3.2 (ESRI, Redlands, California), with all vegetation points located  $\geq 25$  m from each other and the nest.

TABLE 1. Summary information about each field site in the Cumberland Mountains of Tennessee, 2004–2006. The number of years since reclamation was estimated on the basis of vegetative succession and federal documents from the Office of Surface Mining. The number of territorial males is a range based on variation among years.

| Site              | Year of reclamation | Size (ha) | Number of territories year <sup>-1</sup> | Number of nests |
|-------------------|---------------------|-----------|--|-----------------|
| Ash Log Mountain  | ~1990               | 125       | 35–40                                    | 44              |
| Bootjack Mountain | ~1980               | 50        | 12–15                                    | 20              |
| Burge Mountain    | ~1990               | 50        | 12–17                                    | 22              |
| Fork Mountain     | ~1980               | 40        | 12–15                                    | 16              |

In each vegetation plot, we recorded the number of snags (i.e., a dead tree with >5 cm diameter at breast height [DBH]) and estimated average shrub and sapling height (m). We used an ocular tube (James and Shugart 1970) to determine the percent cover of vines, forbs, grass, shrubs, saplings, and canopy trees (trees were defined at those >10 cm DBH). Ocular-tube readings were taken at 20 points within the 11.3-m plot along four transects in the cardinal directions (five readings per transect). Observers recorded the presence of each cover type when looking through the

ocular tube downward from the line of sight 45° and straight up at each point. Ocular-tube readings provided an objective measure of percent cover within plots (number of readings with cover type/20\*100%). Within 1 m of the plot center (which was a nest for nest sites), we also visually estimated the percent cover of grass, forbs, and woody vegetation.

To locate Golden-winged Warbler nests, we observed male and female behavior, especially during nest-building and nestling periods, when bird visits to the nests were frequent. We opportunistically located nests during the laying and incubation periods while systematically walking through territories and while mapping male territory boundaries. We found most of the nests (~70%) during the nest-building stage. We monitored all nests every two to four days until the nestlings fledged or the nest failed.

*Nest-site-selection data analysis.*—We compared vegetation characteristics at nests and randomly selected non-nest sites within Golden-winged Warbler territories using Student's *t*-tests in JMP statistical software, version 6.0 (SAS Institute, Cary, North Carolina). Several variables did not meet the assumption of normality, but our sample sizes for each group (nests,  $n = 102$ ; non-nests,  $n = 188$ ) were large, such that non-normality was considered not to be an issue according to the central-limit theorem (Samuels and Witmer 1999). We compared nine vegetation characteristics and used a Bonferroni adjustment (Samuels and Witmer 1999) to determine significant differences (adjusted  $\alpha = 0.006$ ). Specifically, we compared the number of snags, basal area, and percent cover of saplings, shrubs, forbs, and grass within an 11.3-m sampling plot at nest and non-nest sites. Within a 1-m sampling plot, we also compared the percent cover of woody vegetation, forb, and grass cover between nest and non-nest sites.

*Nest-survival data analysis.*—We modeled the relationship between DSR and several variables based on *a priori* hypotheses, and we used a hierarchical modeling procedure with four suites of models (Table 2) and Akaike's information criterion ( $AIC_c$ ) as the model-selection criteria (Burnham and Anderson 2002). We decided *a priori* to carry over any model that had a  $\Delta AIC_c$  value  $< 2$  to be included in the next suite of models. The use of 2 as a threshold value was suggested by Burnham and Anderson (2002) and was shown to be conservative by Richards (2005). The first set of models considered the influence of two grouping parameters (site and year) on DSR. Annual variation in nest survival was expected because of changes in regional weather patterns and annual fluctuations in predator abundance. Likewise, intersite variation in nest survival was expected if there were differences in vegetation, microclimate, or predator communities among sites.

The second set of models assessed the influence of two climate covariates (minimum daily temperature and mean daily precipitation), nest stage (laying, incubation, brooding), and whether DSR varied linearly or quadratically with date and nest age (Table 2). We hypothesized that low temperatures and precipitation could affect DSR by forcing the female to incubate or brood less often than necessary, as has been demonstrated in previous studies (Siikamäki 1996, Radford et al. 2001; but see Chase 2002). We obtained temperature and precipitation data from the National Oceanic and Atmospheric Administration (NOAA) Climatic Data Center (station no. 723246, KOQT, Oak Ridge). This station was located ~25 km south of the study sites and ~550 m lower in elevation. Because of the difference in

TABLE 2. Descriptions of the four suites of models (I–IV) for daily-nest-survival rate and the corresponding notation. Constant-survival models ( $S_c$ ) containing the intercept only and global models ( $S_{\text{global}}$ ) containing all parameters in a given suite are not included.

| Model suite | Variables                            | Notation                        |
|-------------|--------------------------------------|---------------------------------|
| I.          | Year                                 | $S_{\text{(year)}}$             |
|             | Site                                 | $S_{\text{(site)}}$             |
|             | Year and site                        | $S_{\text{(year + site)}}$      |
| II.         | Linear time                          | $S_{\text{(T)}}$                |
|             | Quadratic time                       | $S_{\text{(TT)}}$               |
|             | Minimum temperature                  | $S_{\text{(mintemp)}}$          |
|             | Daily precipitation                  | $S_{\text{(precip)}}$           |
|             | Temperature and precipitation        | $S_{\text{(mintemp + precip)}}$ |
|             | Nest stage (laying–incubation–brood) | $S_{\text{(stage)}}$            |
|             | Linear age                           | $S_{\text{(age)}}$              |
|             | Quadratic age                        | $S_{\text{(age2)}}$             |
| III.        | Sapling and shrub cover              | $S_{\text{(saps + shrubs)}}$    |
|             | Distance to forest edge              | $S_{\text{(dedge)}}$            |
|             | Grass and forb cover                 | $S_{\text{(grass + forbs)}}$    |
| IV.         | Woody stem in nest substrate (0/1)   | $S_{\text{(subwood)}}$          |
|             | Grass cover within 1 m of nest       | $S_{\text{(mgrass)}}$           |
|             | Forb cover within 1 m of nest        | $S_{\text{(mforb)}}$            |
|             | Woody vegetation within 1 m of nest  | $S_{\text{(mwood)}}$            |
|             | Nest height                          | $S_{\text{(nesthtg)}}$          |

elevation, there were likely differences in the minimum temperature and precipitation on the study sites compared with the Oak Ridge data, but the data were likely correlated with the actual study-site values.

Other studies have demonstrated that nest survival decreases over time and within a season (Grant et al. 2005, Davis et al. 2006; but see Farnsworth et al. 2000), and Grant et al. (2005) documented that DSR varies with time, such that a quadratic or cubic function fits the relationship best. We hypothesized that Golden-winged Warbler DSR may decrease linearly or show a quadratic relationship with time because of increased activity of ground-nest predators as the breeding season progresses. We also tested for a relationship between DSR, nesting stage, and nest age. These parameters are related but differ enough that we tested for each effect independently. The nest-stage model assumes that DSR is constant within a stage. However, survival may vary within the brooding stage, because activity near the nest may be greatest near the end of this stage, thus attracting predators. The DSR may then be relatively unchanged throughout the nesting cycle and decrease toward the end of the brooding stage. In this scenario, a model of nest age is more appropriate than a model of nest stage that assumes constant survival within a stage.

The third and fourth sets of models assessed how DSR varied with vegetation around the nest at the 11.3-m plot level and within 1 m of the actual nest, respectively. Because Golden-winged Warblers occupy a broad range of successional seres, from very open with scattered woody vegetation to mature woodlands with an herbaceous understory, it is not known whether there is a reproductive advantage to any portion of this continuum (i.e., whether DSR varies with the cover of herbaceous and woody vegetation). Therefore, these vegetation-specific models of DSR are somewhat

exploratory, because our models do not test specific hypotheses (i.e., increased shrub cover may increase or decrease DSR). At the plot level, we considered the following three parameters: distance to forest edge, percent cover of herbaceous vegetation (additive model with forb and grass cover), and percent cover of woody vegetation (additive model with sapling and shrub cover) (Table 2). At the nest-site level (1-m sub-plot), we considered the following parameters: nest height, presence of a woody stem in the nest substrate, and percent cover of woody vegetation, grass, and forbs. Although Golden-winged Warblers nest on the ground, there is some variation in the height of the nest rim related to the size of the nest and the type of substrate in which the nest is built. We hypothesized that nests that extend farther off the ground and have a woody stem in the substrate may be more visible to predators than nests with all materials closer to the ground and, therefore, have lower DSR.

*Nest-survival modeling procedure.*—We used the nest-survival module in MARK (White and Burnham 1999, Rotella et al. 2004) to compare nest-survival models and to obtain estimates of daily nest survival. With the logit link, DSR on day *i* is modeled as

$$DSR = \frac{\exp(\beta_0 + \sum_j \beta_j x_{ji})}{(1 + \exp(\sum_j \beta_j x_{ji}))}$$

where the  $x_{ji}$  ( $j = 1, 2, \dots, J$ ) are values for *j* covariates on day *i* and the  $\beta_j$  are coefficients to be estimated from the data (Rotella et al. 2004). We assumed a 25-day nesting cycle for Golden-winged Warblers, with 4 days for laying, 11 days for incubation, and 10 days for brooding (Ehrlich et al. 1988, Confer 1992). Year ( $n = 3$ ), site ( $n = 4$ ), and nest stage ( $n = 3$ ) were modeled as groups in the nest-survival module, resulting in 36 groups. For each nest, we also included 65 individual covariates. The two climatic variables and eight vegetation variables accounted for 10 of the covariates, and the remaining 55 covariates accounted for daily age of the nest across the nesting cycle. Throughout the three years of study, Golden-winged Warbler nests were active from 5 May (first egg date) to 28 June, for a 55-day nesting season. Data structure and entry followed those of Dinsmore et al. (2002). As suggested by Dinsmore et al. (2002) and Rotella (2007), we did not standardize individual covariates, because the unstandardized covariates did not affect numerical optimization.

Within each model set, we decided *a priori* to create an additional additive model using all variables from models that have  $\Delta AIC_c$  values  $< 2$ . Models meeting the  $\Delta AIC_c < 2$  criterion should not be ruled out as being the best model given the data (Burnham and Anderson 2002). We also decided *a priori* to carry over any models with  $\Delta AIC_c$  values  $< 2$  onto the next suite of models. We did this to allow for combinations of important variables from the different suites of models without having to run all possible subsets with all possible variables. We chose variables of interest *a priori*, as well as the criteria for future combinations of variables; we believe that this framework leads to more parsimonious model subsets than the alternative of running hundreds of models for a single analysis and, thus, running the risk of obtaining spurious results.

TABLE 3. Mean values ( $\pm$  SE) of nine vegetation characteristics at nest sites and randomly selected non-nest sites within Golden-winged Warbler territories in the Cumberland Mountains, Tennessee, 2004–2006. Parameters with asterisks were significantly different ( $P < 0.05$ ), and those with double asterisks were significant after the Bonferroni adjustment ( $P < 0.006$ ).

| Scale                            | Vegetation parameter        | Nests          | Non-nests      | <i>P</i> |
|----------------------------------|-----------------------------|----------------|----------------|----------|
| Plot level<br>(11.3-m<br>radius) | Basal area                  | 21.1 $\pm$ 2.0 | 18.2 $\pm$ 1.5 | 0.348    |
|                                  | Number of snags*            | 6.7 $\pm$ 0.4  | 5.3 $\pm$ 0.3  | 0.014    |
|                                  | Percent cover grass*        | 70.2 $\pm$ 2.5 | 62.4 $\pm$ 1.9 | 0.012    |
|                                  | Percent cover forbs         | 79.1 $\pm$ 1.8 | 78.7 $\pm$ 1.3 | 0.843    |
|                                  | Percent cover shrubs        | 36.5 $\pm$ 2.6 | 42.7 $\pm$ 1.9 | 0.077    |
|                                  | Percent cover<br>saplings** | 31.4 $\pm$ 2.8 | 44.5 $\pm$ 2.1 | <0.001   |
| Subplot<br>level<br>(1-m radius) | Percent cover<br>woody**    | 34.5 $\pm$ 3.0 | 47.2 $\pm$ 2.2 | <0.001   |
|                                  | Percent cover forbs**       | 49.3 $\pm$ 2.6 | 39.9 $\pm$ 1.9 | 0.003    |
|                                  | Percent cover grass**       | 52.3 $\pm$ 3.0 | 39.3 $\pm$ 2.2 | <0.001   |

**RESULTS**

We monitored 102 Golden-winged Warbler nests during the 2004–2006 breeding seasons for 1,613 exposure days across a 55-day interval. Sixty of these nests were successful (58.8%), and 40 of the 42 failed nests (>95%) were attributed to predation. There was no evidence of double-brooding. The mean ( $\pm$  SE) age of nests when found was 5.60  $\pm$  0.66 days; 70% of all nests were found before incubation began (during construction).

*Nest-site selection.*—Of the nine vegetation variables assessed, four differed between nests and randomly selected non-nest sites within Golden-winged Warbler territories, based on the Bonferroni adjustment (Table 3). The percent cover of saplings in the 11.3-m-radius plot and the percent cover of woody vegetation, forbs, and grass within a 1-m-radius plot differed ( $P < 0.006$ ) between nest and non-nest plots. Nest sites had more grass and forb cover at the 1-m-plot scale, fewer saplings at the 11.3-m-plot scale, and less woody cover at the 1-m-plot scale (Table 3).

*Nest survival.*—In the first set of models assessing the effects of study site and year, the constant-survival model had the most support ( $AIC_c$  weight [ $w$ ] = 0.57), which indicates that daily nest survival may not vary significantly across sites and years in Golden-winged Warblers (Table 4). However, the model with a

TABLE 4. Summary of model-selection results from the first suite of models for nest survival of Golden-winged Warblers in the Cumberland Mountains of Tennessee, 2004–2006. Model notation is described in Table 2. The  $AIC_c$  values are different in this suite than in future suites for the exact same models because the nest-stage grouping effect was removed.

| Model               | <i>K</i> | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---------------------|----------|---------|----------------|-------|
| $S_{(.)}$           | 1        | 312.32  | 0              | 0.565 |
| $S_{(year)}$        | 3        | 313.30  | 0.98           | 0.347 |
| $S_{(site)}$        | 4        | 317.10  | 4.78           | 0.052 |
| $S_{(year + site)}$ | 6        | 317.84  | 5.51           | 0.036 |

TABLE 5. Estimated daily-nest-survival rates (DSR), by year and site, for Golden-winged Warblers in the Cumberland Mountains, Tennessee, 2004–2006. Differences among sites are marginal, whereas annual variation in DSR is more apparent.

| Nuisance parameter | Mean DSR | SE     | 95% CI |        |        |
|--------------------|----------|--------|--------|--------|--------|
|                    |          |        | Lower  | Upper  |        |
| Site               | Ash Log  | 0.9753 | 0.005  | 0.9616 | 0.9842 |
|                    | Bootjack | 0.9783 | 0.009  | 0.9526 | 0.9902 |
|                    | Burge    | 0.9752 | 0.009  | 0.9489 | 0.9881 |
|                    | Fork     | 0.9635 | 0.012  | 0.9313 | 0.9809 |
| Year               | 2004     | 0.9834 | 0.006  | 0.9656 | 0.9921 |
|                    | 2005     | 0.9738 | 0.006  | 0.9597 | 0.9830 |
|                    | 2006     | 0.9641 | 0.009  | 0.9403 | 0.9786 |

year effect also had support ( $\Delta AIC_c = 0.98$ ,  $w = 0.35$ ), which suggests that there may be some degree of annual variation in DSR. The actual estimates of annual DSR (Table 5) overlapped considerably, and the confidence intervals for the year-effect beta coefficients included zero. In our modeling approach, only the year effect was added to the second suite of models.

In the second set of models, a constant-survival model was again most supported by the data ( $w = 0.19$ ); however, several models that had  $\Delta AIC_c$  values  $< 2$  were added to the third suite of models: the linear and quadratic time variables and minimum temperature, year, and daily precipitation. In the third set of models, these same parameters had  $\Delta AIC_c$  values  $< 2$ , in addition to a model with the percent cover of shrubs and saplings and another model with distance to forest edge. For the final set of models, several had  $\Delta AIC_c$  values  $< 2$  (Table 6), but parameter estimates for all covariates included zero (Table 7), and the constant-survival model had equal support. We did not use model averaging to

TABLE 6. Summary of model-selection results from the final set of models for nest survival of Golden-winged Warblers in the Cumberland Mountains, Tennessee, 2004–2006. Model notation is described in Table 2.

| Model   | K  | AIC <sub>c</sub> | $\Delta AIC_c$ | $w_i$ |
|---|----|------------------|----------------|-------|
| S <sub>(subwood)</sub>  | 2  | 318.22           | 0              | 0.136 |
| S <sub>(.)</sub>  | 1  | 318.35           | 0.13           | 0.128 |
| S <sub>(minTemp)</sub>  | 2  | 318.43           | 0.21           | 0.123 |
| S <sub>(T)</sub>  | 2  | 318.99           | 0.78           | 0.092 |
| S <sub>(saps + shrubs)</sub>  | 3  | 319.11           | 0.90           | 0.087 |
| S <sub>(TT)</sub>   | 3  | 319.52           | 1.30           | 0.071 |
| S <sub>(mgrass)</sub>   | 2  | 319.78           | 1.56           | 0.062 |
| S <sub>(year)</sub>   | 3  | 320.08           | 1.86           | 0.054 |
| S <sub>(precip)</sub>   | 2  | 320.15           | 1.94           | 0.052 |
| S <sub>(dedge)</sub>  | 2  | 320.18           | 1.96           | 0.051 |
| S <sub>(mwood)</sub>  | 2  | 320.29           | 2.07           | 0.048 |
| S <sub>(Nesthtg)</sub>  | 2  | 320.34           | 2.12           | 0.047 |
| S <sub>(mforb)</sub>  | 2  | 320.35           | 2.13           | 0.047 |
| S <sub>(subwood + minTemp + T + TT + saps + shrubs + mgrass + year + precip + dedge)</sub>                            | 12 | 327.77           | 9.55           | 0.001 |
| S <sub>(subwood + minTemp + T + TT + saps + shrubs + mgrass + year + precip + dedge + Nesthtg + mwood + m forb)</sub> | 15 | 332.13           | 13.91          | 0.000 |

TABLE 7. Beta estimates and 95% confidence intervals (CI) for parameters in the top models (i.e., those with  $\Delta AIC$  values  $< 2$ ) in the final and fourth set of models for nest survival of Golden-winged Warblers in the Cumberland Mountains, Tennessee, 2004–2006.

| Parameter                    | Estimate | 95% CI  |        |
|------------------------------|----------|---------|--------|
|                              |          | Lower   | Upper  |
| Woody stem as nest substrate | -0.458   | -1.072  | 0.1562 |
| Linear time                  | -0.018   | -0.0477 | 0.0120 |
| Quadratic time               | -0.001   | -0.0035 | 0.0008 |
| Sapling cover                | -0.008   | -0.0197 | 0.0029 |
| Shrub cover                  | 0.010    | -0.0042 | 0.0241 |
| Grass cover in 1 m           | 0.004    | -0.0071 | 0.0161 |
| Minimum temperature          | -0.033   | -0.0797 | 0.0145 |
| Daily precipitation          | -0.301   | -1.2938 | 0.6914 |
| Distance to forest edge      | -0.003   | -0.0141 | 0.0091 |

obtain estimates of covariate effects, because covariates were not typically present in more than one model.

Our model-selection results provided some evidence that DSR decreased as daily minimum temperature increased, decreased over time, increased with increasing shrub cover, and decreased with increasing sapling cover. In addition, presence of a woody stem in the nest substrate performed better than the constant-survival model, such that nests with a woody stem had a lower DSR (0.9663) than nests without a woody stem (0.9784). The AIC weights for this model and the constant-survival model, however, were very similar (Table 6). The estimate for Golden-winged Warbler DSR from the constant-survival model was  $0.973 \pm 0.004$ .

## DISCUSSION

*Nest-site selection.*—Golden-winged Warbler nest-site selection appears to be nonrandom, such that females select nest sites with specific habitat attributes. Nest sites had more grass and forb cover and less woody vegetation cover within 1 m and had fewer saplings within 11.3 m (Table 3). In theory, female Golden-winged Warblers should select nest-site characteristics that reduce the probability of nest predation (Martin 1988b). This hypothesis would be supported if similar habitat attributes affected nest-survival rates, as demonstrated by Martin (1998). However, recent studies have demonstrated no apparent relationship between nest-site selection and nest survival (Wilson and Cooper 1998, Wilson and Gende 2000, Siepielski et al. 2001). Likewise, we did not find any habitat variables, except potentially one (the presence of a woody stem in the nest substrate), that seemed to influence nest survival rates (see below). Golden-winged Warblers on our study sites may simply effectively identify nesting sites with low predation rates. Alternatively, the habitat characteristics associated with Golden-winged Warbler nest sites in the Cumberland Mountains may be more a reflection of resource partitioning or females optimizing their chances for extrapair copulation (Westneat and Mays 2005) than a mechanism for optimizing nest survival. Females that place their nests near territory boundaries have an increased probability of having extrapair young with a neighboring male (Westneat and Mays 2005). Martin (1988a) suggested that bird species partition

nest sites because of density-dependent predation pressures, allowing for coexistence of similar species. Regardless of the mechanism or degree to which it is adaptive, Golden-winged Warblers appear to select nest sites with specific habitat attributes, and ensuring the presence of these nest-site characteristics in the landscape is important for the conservation of this species.

*Nest survival.*—Our results did not identify any strong relationships between the factors we considered and daily nest survival. All parameter estimates included zero, only one model performed better than the constant-survival model, and that model actually had equal support (i.e.,  $AIC_c$  weight). However, several models had  $\Delta AIC_c$  values  $< 2$ , which suggests that of the models considered, these variables may have some effect on daily nest survival. Our sample of 102 nests, with 40 depredated, may provide too few data to support these alternative nest-survival models. Despite the lack of a strong effect for any one model, we briefly discuss the models that had some support (i.e., those with  $\Delta AIC_c < 1$ ).

The DSR tended to decrease with increasing minimum daily temperature and to decrease over time, but the constant-survival model performed equally well as models with either of these covariates. These two covariates were also correlated; as the nesting season progressed, daily minimum temperature increased. We predicted the opposite trend, with lower nest survival when temperatures were cooler. An alternative explanation is that nest-predator activity increases throughout the nesting season as temperatures rise. Small mammals (Söderström et al. 1998) and snakes (Thompson and Burhans 2003, Weatherhead and Blouin-Demers 2004) make up the dominant nest-predator community for ground-nesting birds such as Golden-winged Warblers. Snakes are abundant on our study sites and do not typically become active until later in the season, when the temperatures have risen and more food is available (Stake et al. 2005, L. Bulluck pers. obs.). More study is needed regarding the specific causes of nest failure in Golden-winged Warblers (i.e., frequencies of predation by specific predators). Studies that address predation of songbird nests should explore further the relationship between time of season and nest-predator activity.

A model with two covariates representing sapling and shrub cover in the 11.3-m plot was also supported ( $\Delta AIC_c < 2$ ). The DSR increased as shrub cover increased and decreased as sapling cover increased (Fig. 1C–D); however, the parameter estimates for these covariates included zero. We did not have specific *a-priori* hypotheses regarding these vegetation components. A previous study of Golden-winged Warblers in New York demonstrated that shrub cover was positively related to clutch size (Confer et al. 2003). The influence of vegetation structure on Golden-winged Warbler DSR, if any, requires more study, because there may be vegetative parameters that could be managed to increase DSR.

Only one model with one habitat covariate (the presence of a woody stem as the nest substrate) performed better than the constant-survival model (i.e., it had a greater model weight). However, the parameter estimate for this covariate included zero, and the model weights for this model and the constant-survival model were similar. This suggests that the presence of a woody stem in the nest substrate may not significantly affect DSR.

Our model results suggest that (1) nest predation may be a random process in this system, (2) Golden-winged Warblers

consistently select sites with low predation rates, or (3) predation is a dynamic and complex process driven by myriad factors, some of which were not measured in the present study. Other studies of avian nest success have speculated that predation may be random (Holway 1991, Filliater et al. 1994, Howlett and Stutchbury 1997, Wilson and Cooper 1998). However, there are other possible reasons why habitat factors appear to be unrelated to DSR. Although our four study sites are different (Table 1), there may be too little variation in habitat types across these sites to display a difference in DSR from our sample of nests. Our study sites represented a large portion of the broad successional spectrum that Golden-winged Warblers occupy, though the extremes were not present. Drastic increases or decreases in nest survival may occur in habitat components present in these extremes. Finally, we may not have measured the appropriate variables that truly affected Golden-winged Warbler nest survival.

Other studies of factors influencing avian nest survival have found little or no effect of microhabitat or vegetation (Filliater et al. 1994, Wilson and Cooper 1998, Huhta et al. 1999, Wilson and Gende 2000, Siepielski et al. 2001, Burhans et al. 2002, Chase 2002, Davis 2005). Several hypotheses for this have been presented. Temporal factors may be at play, such that current nest-site-selection criteria may reflect historical predator communities and densities (Martin 1988a, Siepielski et al. 2001). Indeed, Misenhelter and Rotenberry (2000) found that birds preferred to nest in areas in which they did not reproduce successfully (i.e., an “ecological trap”), perhaps caused by the redistribution of nest predators following anthropogenic disturbance. Alternatively, spatial and temporal variation in predation may lessen the response of a species to natural-selection pressures, leading to the lack of a strong relationship between nest-site characteristics and nest survival (Chase 2002). Nest-site selection may also be controlled by factors other than nest predation, such as food availability (Lenington 1980), foraging efficiency (Huhta et al. 1999), or landscape-level factors (Rodewald and Yahner 2001).

The relationships suggested by the present study provide an excellent pool of potential hypotheses to test, both within the Cumberland Mountains population of Golden-winged Warblers and throughout the species’ range. Conservation of this declining species depends, in part, on our understanding of factors related to nest survival. Until the mechanisms behind these factors are better understood, habitat-based management approaches to increasing nest survival may be ineffective.

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