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Do Golden-cheeked Warblers Select Nest Locations on the Basis of Patch Vegetation?

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ABSTRACT.—Proper management of endangered species requires an understanding of habitat use at a variety of spatial scales, and information on nesting habitat is especially important in that regard. We examined vegetation features associated with nest patches of the Golden-cheeked Warbler (*Dendroica chrysoparia*), a federally endangered migrant songbird that breeds only in central Texas. We used a spatially paired design to measure 13 vegetation variables at 43 nests and at an equal number of randomly chosen nonuse patches, one located near each nest. Canopy closure was greater at nest patches than at nonuse patches. However, none of the other vegetation variables differed between a nest patch and its paired nonuse patch on the same territory, despite high power to detect such differences. In contrast, 8 of the 13 variables exhibited significant variation among territories. For all 13 variables, effect size was substantially greater for variation between territories than for variation between nest patches and their paired nonuse patches. Lack of within-territory variation may reflect the scale at which vegetation varies in that habitat. Such a result suggests that territory selection may be more important than nest-patch selection in this species.

Information on habitat use is critical for making proper management decisions (Verner et al. 1986). That is particularly true for endangered species, whose populations are often limited by availability of suitable habitat (Mayfield 1963, Scott et al. 1986, Jackson 1994). For birds, selection of nesting habitat is especially important, because nest location often affects reproductive success (Martin 1992, 1998) and, thus, population viability.

Defining "suitable habitat" requires a recognition that habitat selection is often hierarchical, especially when studying habitat used for a specific behavior such as nesting (e.g. Martin 1992, Steele 1993, Murphy et al. 1997). Nesting habitat can be quantified at a very broad scale (i.e. habitat features associated with presence or absence of a species), at the level of territory placement, at the level of nest patch within the territory, and, finally, as specific attributes of the nest site. Describing vegetation features associated with the nest patch is one of the key components of quantifying avian habitat requirements, particularly

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for endangered species with limited breeding habitat.

We examined nest-patch vegetation of the Golden-cheeked Warbler (*Dendroica chrysoparia*), a federally endangered migratory songbird. Golden-cheeked Warblers breed in short woodland habitat dominated by Ashe juniper (*Juniperus ashei*) and oaks (Ladd and Gass 1999). That habitat is restricted to limestone hills and canyons of central Texas (Kier et al. 1977). Loss of that habitat due to ranching and urban development is the primary reason the Golden-cheeked Warbler was designated as endangered (U.S. Fish and Wildlife Service 1990, 1992).

Golden-cheeked Warblers build nests approximately 3–7 m off the ground, typically in Ashe juniper but sometimes in oaks or other hardwoods, and nests are constructed primarily from bark strips peeled from the trunks of mature Ashe junipers (Ladd and Gass 1999). Previous researchers have suggested that breeding habitat for Golden-cheeked Warblers must include dense, close-canopied oak–juniper woodlands containing large juniper trees (Ladd and Gass 1999); however, no quantitative comparisons have been made between nest patches and unused patches available for nesting. As an initial step in understanding nesting-habitat requirements of Golden-cheeked Warblers, we quantified vegetation features of nest patches and tested whether those vegetation features differed from those of nearby patches that were not used for nesting.

Methods.—We studied Golden-cheeked Warblers on Fort Hood, an 88,500 ha active U.S. Army installation in central Texas. Fort Hood contains the largest Golden-cheeked Warbler breeding population under a single management agency, thus making it a critical area from a conservation standpoint.

Fort Hood consists of a mix of grassland, open savannah, hardwood thickets, and dense oak–juniper stands (Tazik et al. 1993, Jetté et al. 1998). On Fort Hood, Golden-cheeked Warblers are typically found in oak–juniper woodlands, which are dominated by Ashe juniper, plateau live oak (*Quercus fusiformis*), Texas red oak (*Q. buckleyi*), shin oak (*Q. sinuata*), Texas white ash (*Fraxinus texensis*), and cedar elm (*Ulmus crassifolia*). Fort Hood contains ~21,850 ha of suitable Golden-cheeked Warbler breeding habitat, based upon criteria of at least 75% canopy closure, a mix of junipers and hardwoods, and a contiguous stand of at least 1 ha (J. Horne unpubl. data).

Researchers have speculated that Golden-cheeked Warblers require a mix of Ashe junipers and hardwoods for breeding (Ladd and Gass 1999). Junipers are necessary for nest materials (Pulich 1976), and there is some evidence that both junipers and hardwoods are needed for foraging (Beardmore 1994). Because of interest in relative importance of junipers and hardwoods to those birds, part of our vegetation analysis is devoted to examining these plant groups separately.

Vegetation measurements were made at 43 nests from 1993–1997 ($n = 7$ in 1993, $n = 9$ in 1994, $n = 6$ in 1995, $n = 11$ in 1996, and $n = 10$ in 1997). Sampling design and subsequent analysis were paired, such that vegetation measurements were made at a nest patch and at a randomly chosen nonuse patch near the nest. Nonuse patches were selected by measuring either 30, 40, or 50 m (randomly chosen) in a random direction from the nest. That distance assures independence of samples but almost always places the nonuse patch in the same territory as the nest, because average territory size at Fort Hood is 4.15 ha (Weinberg et al. 1996) and territories are roughly circular, rather than linear (based on spot-mapping of color-banded birds; A. Anders unpubl. data). Thus, the nonuse patch can be justifiably viewed as a location in which a particular breeding pair chose not to place a nest. Selection of the nonuse patch was strictly random—no attempt was made to subjectively choose a patch that looked "suitable for" or "similar to" a nest patch on the basis of the researcher's perception of habitat.

At both the nest and nonuse locations, vegetation variables were measured in a circular plot with a radius of 11.3 m and an area of 0.04 ha. We measured canopy closure, number of juniper and hardwood trees, and foliage cover of junipers and hardwoods. Canopy closure was measured with a densiometer by averaging four readings taken at the center of the plot, one in all four cardinal compass directions. Number of trees in the plot was determined separately for Ashe junipers and all hardwoods, and separate tallies were kept for three diameter at breast height (DBH) size classes: 7.6–15.1 cm, 15.2–22.8 cm, and >22.8 cm. Trees in that arid, shallow-soil habitat are typically small, with heights often <8 m and DBH often <23 cm.

Foliage cover was measured with a range pole at 20 points within the 0.04 ha plot. Points were arrayed every 2 m along the north–south and east–west axes of the plot. The range pole was divided into 10 cm increments below 3 m, and 50 cm increments above 3 m. At each of the 20 sampling points in the plot, presence or absence of woody vegetation contacting the range pole within each increment was recorded. For analysis, we collapsed those measurements into three height classes based on our impression of habitat structure and on the behavior of Golden-cheeked Warblers: 0–2 m, 2–4.5 m, and >4.5 m. Golden-cheeked Warblers rarely forage below 2 m, and the maximum canopy height is often ≤4.5 m. Within each height class, we recorded proportion of increments in which woody vegetation contacted the range pole. Scores were averaged across all 20 points in a particular sampling plot. Separate scores were computed for Ashe junipers and for all hardwoods combined.

Most of the 13 vegetation variables required transformation (log, square-root, or arcsin-square-root, depending on distribution) to achieve normality prior to parametric analysis. Mean values presented in this paper are back-transformed to their original units after analysis.

Our analysis takes advantage of the paired nature of our samples. That is important because our impression (later borne out by these analyses) was that most vegetation features of that habitat vary at a large, rather than small, spatial scale; in other words, large variation between territories would swamp out differences between nest patches and nonuse patches if a paired analysis was not used.

We first tested for differences between years. For each of the vegetation variables, we computed a difference score by subtracting the value at nest patch from the value at its paired nonuse patch. Using a one-way MANOVA, we tested whether differences between nest patches and nonuse patches varied between years. No such variation was found (Hotelling's $T = 1.58$, $F = 0.74$, df = 52 and 98, $P = 0.88$). Thus, years were pooled for subsequent analyses.

We used a two-way unreplicated MANOVA, in which patch (nest vs. nonuse) was a fixed factor and territory (i.e. a separate level of the factor for each territory) was a random factor. We had 13 dependent variables: canopy closure, number of trees per plot in three DBH classes and two species classes, and vegetation foliage cover at three height intervals for two species classes. After the overall MANOVA, we performed separate univariate ANOVA for each vegetation variable, using the same two-way design and a Bonferroni-adjusted alpha ($\alpha = 0.05/13 = 0.004$). The unreplicated design requires the assumption of no interaction between the two factors because residual variation is used as the error term for tests of main effects (Sokal and Rohlf 1995). We used Tukey's test for additivity to test this assumption of no interaction (Neter et al. 1990). This assumption was met for all variables except canopy closure. The effect of violating that assumption is reduced power (Neter et al. 1990); because we did detect a main effect of canopy closure, violation of the assumption is not important in this instance.

The test for patch effect (nest vs. nonuse) in this two-way unreplicated design is analogous to the use of a paired t-test. The advantage of the ANOVA design is that it allows for comparison of the effect size of within- versus between-territory variation. *Post-hoc* power analyses were computed as for paired t-tests (Zar 1996). For those power analyses, we specified a desire to detect a minimum difference of 15% (on the untransformed variables) between nest patches and nonuse patches, and we used our own sample size and our own data for mean difference scores between paired nest patches and nonuse patches and for the variance of those difference scores. Our choice of a 15% difference for power analysis was arbitrary, but that value is smaller than many observed differences reported in other studies of avian nesting habitat.

Results.—The overall MANOVA detected a slightly nonsignificant difference between nest patches and nonuse patches (Hotelling's $T = 0.81$, $F = 1.88$, df = 13 and 30, $P = 0.075$) and a highly significant difference among territories (Hotelling's $T = 44.27$, $F = 2.28$, df = 546 and 366, $P < 0.001$).

In the univariate ANOVA, canopy closure was the only variable that differed between nest patches and nonuse patches (Table 1): nest patches had greater canopy closure than nonuse patches. In contrast, there was significant variation between territories in 8 of the 13 vegetation variables (Table 1). For all 13 variables, effect size (as measured by partial eta-squared) was substantially greater for variation between territories than for variation between nest patches and their paired nonuse patches (Table 1). For the 12 variables in which we found no difference between nest patches and nonuse patches, average power was 0.891 (range 0.136–1.00) to detect a 15% difference, and average power was 0.966 (range 0.578–1.00) to detect a 25% difference; power was below 0.8 only for detecting a difference in number of small juniper trees per plot.

Discussion.—Golden-cheeked Warbler nests were located in patches of dense vegetation characterized by nearly complete canopy closure. Nest patches had a high density of small trees (equivalent to 487 trees per hectare for hardwoods and junipers combined), and small junipers were nearly twice as prevalent as small hardwoods. Junipers were more common than hardwoods in medium and large DBH classes as well. Woody foliage cover, as measured by range-pole contacts, was high for junipers between 2 and 4.5 m above the ground and also for junipers >4.5 m above the ground. Woody foliage cover was lower, and similar across categories, for junipers below 2 m and for hardwoods in all height classes. Thus, in general, warbler nest patches were characterized by closed canopy, many small trees (particularly junipers), and dense juniper cover above a height of 2 m.

Because this is the first characterization of nest patch vegetation for this endangered songbird, no comparative data are available from other parts of its breeding range. However, researchers have assessed general features of Golden-cheeked Warbler habitat in other parts of central Texas, and those studies indicate some similarities to nest-patch vegetation at Fort Hood. For example, many researchers have emphasized importance of a high density of Ashe junipers for Golden-cheeked Warblers (reviewed in Ladd and Gass 1999), and several authors have suggested that dense, close-canopied woodland may be important for these birds (Ladd 1985, U.S. Fish and Wildlife Service 1992). Although Ladd and Gass (1999) suggested that presence of older junipers may be a critical determinant of habitat selection by Golden-cheeked Warblers, we found that nest patches contained high densities of small, presumably young, junipers. More detailed comparisons with other studies are prohib-

TABLE 1. Results of univariate two-way ANOVAs for 13 vegetation variables. Means (95% family-wide CI) are back-transformed to original units. *indicates significance after standard Bonferroni adjustment. Power is calculated for detecting a 15% difference between nest patch and nonuse patch. Power is 0.578 for detecting a 25% difference in number of small junipers between nest patch and nonuse patch.

			Between territories			Nest vs. nonuse (within territories)			
Variable	Mean at nest	Mean at nonuse	F^a	P	eta^2	F^b	P	eta^2	Power
Canopy closure (%)	93.9 (90.2 to 96.8)	83.6 (69.9 to 93.7)	1.27	0.218	0.560	9.69	0.003*	0.187	0.999
No. juniper trees, 7.6–15.1 cm dbh, per plot	12.7 (8.4 to 16.9)	14.6 (10.3 to 18.9)	5.24	<0.001*	0.840	3.00	0.091	0.067	0.136
No. juniper trees, 15.2–22.8 cm dbh, per plot	3.9 (2.4 to 6.1)	4.8 (3.2 to 7.0)	3.28	<0.001*	0.767	2.55	0.118	0.057	0.997
No. juniper trees, >22.8 cm dbh, per plot	4.2 (2.8 to 6.2)	4.0 (2.6 to 5.9)	3.52	<0.001*	0.779	0.27	0.608	0.006	0.994
No. hardwood trees, 7.6–15.1 cm dbh, per plot	6.8 (4.3 to 10.5)	6.5 (3.8 to 10.8)	1.73	0.040	0.633	0.05	0.818	0.001	0.987
No. hardwood trees, 15.2–22.8 cm dbh, per plot	1.5 (0.6 to 2.8)	1.5 (0.7 to 2.4)	3.08	<0.001*	0.755	0.08	0.785	0.002	1.000
No. hardwood trees, >22.8 cm dbh, per plot	0.76 (0.24 to 1.44)	0.89 (0.34 to 1.59)	1.73	0.039	0.634	0.25	0.617	0.006	1.000
Juniper foliage cover, 0–2 m	3.6 (2.3 to 5.4)	4.4 (3.1 to 6.2)	1.70	0.044	0.630	2.00	0.165	0.045	0.969
Juniper foliage cover, 2–4.5 m	8.3 (5.9 to 11.4)	9.4 (6.9 to 12.6)	1.66	0.052	0.624	1.01	0.322	0.023	1.000
Juniper foliage cover, >4.5 m	5.9 (3.0 to 9.7)	4.1 (2.0 to 6.8)	3.05	<0.001*	0.753	3.85	0.056	0.084	0.990
Hardwood foliage cover, 0–2 m	3.4 (2.0 to 5.5)	2.9 (1.9 to 4.2)	3.05	<0.001*	0.753	1.27	0.266	0.029	0.810
Hardwood foliage cover, 2–4.5 m	3.7 (2.3 to 5.7)	3.4 (2.1 to 5.1)	2.72	0.001*	0.731	0.40	0.529	0.009	0.897
Hardwood foliage cover, >4.5 m	4.7 (2.2 to 9.1)	4.2 (2.1 to 7.7)	2.34	0.003*	0.701	0.22	0.641	0.005	0.804

[a] df = 42 and 42.

[b] df = 1 and 42.

ited by differences in methodology and by changes in plant communities across the breeding range of the Golden-cheeked Warbler.

We found minimal differences between vegetation surrounding Golden-cheeked Warbler nests and vegetation in nearby patches that were not used for nesting. The only significant difference between nest patches and nonuse patches was in canopy closure, such that nest patches had more closed canopies than did nonuse patches. That difference, however, is likely an artifact of the sampling procedure, because nests were always in trees and nonuse patches were not necessarily centered at trees because they were selected randomly. We found no other differences between nest patches and nonuse patches, even though our power to detect such differences was generally quite high: to detect a 15% difference between nest patches and nonuse patches (assuming Bonferroni-adjusted α of 0.004), our average power was 0.891. The only variable for which power was <0.8 was number of small juniper trees in the patch (Table 1).

Our sampling scheme of randomly placed nonuse patches (rather than nonuse locations centered on a "suitable" nest plant) would tend to create, rather than obscure, differences between nest patches and nonuse patches. Thus, general similarity between nest patches and neighboring nonuse patches in our study is real. Such a result is unusual, because most studies do find pronounced differences between nest patches and nonuse patches, even when sample sizes are small (e.g. Kilgo et al. 1996, Timoney 1999) or when nonuse locations are deliberately chosen to be similar to nest patches in features such as plant species (e.g. Martin 1998, Burhans and Thompson 1999) or topography (e.g. Martin and Roper 1988, Martin 1998). Similarity between nest patches and nonuse patches in our study might simply reflect the scale at which vegetation varies in that habitat. In other words, there may not be enough vegetative variation between patches within a territory for any measure of vegetation to vary at such a scale. If so, a bird's selection of a territory may be the functional equivalent of its selection of a nest patch.

In contrast to the lack of difference between nest patches and nonuse patches in this study, we did find significant between-territory variation for 8 of the 13 variables measured. In addition, our measure of effect size was substantially greater for between- versus within-territory variation for all 13 variables. This confirms our *a priori* impression that most vegetation features in that habitat vary at a scale equal to or larger than that of an individual Golden-cheeked Warbler territory. As has been seen in other species, vegetation differences between territories could be correlated with differences in other variables such as age of birds, date of territory settlement, and nesting success on the territory (Hill 1988, Aebischer et al. 1996, Curry et al. 2000). Understanding those relationships is important for successful conservation, and a study addressing those issues is currently underway at Fort Hood (A. Anders unpubl. data). Lack of between-territory variation in 5 of the 13 vegetation variables suggests two possibilities: those vegetation features are critical cues used by warblers in choosing their breeding territories, or those features are invariant in the oak–juniper woodlands in that region.

There are additional levels at which selection of nesting habitat may be important for this species. At a small scale, particular nest-site attributes may be related to nesting success. At a larger scale, there are likely to be vegetation variables that predict presence or absence of Golden-cheeked Warblers altogether. Finally, there could be differences in nest-patch vegetation of successful and unsuccessful nests despite a lack of difference between nest patches and nonuse patches. We and our colleagues are currently exploring these hypotheses.

Our data do not point toward any management actions that can be taken to create or preserve appropriate nest patches for Golden-cheeked Warblers on Fort Hood. Delineation of habitat features associated with territory placement and with nest success will be an important next step in successful management and conservation of this species.

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Timing of Mineral Sequestration in Leg Bones of White-tailed Ptarmigan

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ABSTRACT.—Birds are unique among vertebrates in that they protect their eggs with rigid, calcium-rich shells. Thus, for a short period of time during the annual reproductive cycle, birds experience extraordinarily high demands for calcium. Two strategies appear to exist for meeting those temporally high demands. Some birds apparently seek out calcium-rich foods immediately prior to and during egg laying whereas others may store calcium in their skeletons over a much longer period of time, mobilizing those reserves only when they are needed for production of eggshells. In this study, we used dual energy, X-ray absorptiometry and inductively coupled plasma mass spectroscopy to monitor annual shifts in bone mineral content in the legs of White-tailed Ptarmigans (*Lagopus leucurus*). The study organisms were known to live on calcium-poor soils. Despite an apparent shortage of calcium in their diets, the test subjects stored substantial amounts of calcium in their leg bones in months prior to reproduction. Those stores were subsequently depleted during the egg-laying period. We suggest ability to store calcium in the skeleton may afford this species more flexibility in selecting suitable breeding habitats than would be possible otherwise.

In many avian species, eggs are laid at a rate of one per day. Calcium-rich eggshells are formed, one at a time, in the final 24 h before each egg is laid (Romanoff and Romanoff 1949, Simkiss 1961, 1967). The question asked by many researchers in recent years has been, how do birds—particularly those living on calcium-poor soils—ingest enough calcium in the final hours before an egg is laid to meet the extraordinarily high

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