Species Conservation at a Broad Spatial Scale: Reproductive Success of Golden-Cheeked Warblers Across Their Breeding Range

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ABSTRACT Research conducted near the time a species is listed as threatened or endangered can help inform management guidelines. However, these studies are typically limited in temporal and spatial scope and typically address a limited set of ecological questions. Application of such information can result in misleading management guidelines or ineffective conservation if species–habitat relationships vary across space or if preliminary information fails to provide reliable assessments of habitat quality. We evaluated existing management guidelines that addressed reproductive success of the golden-cheeked warbler (Setophaga chrysoparia), a federally endangered songbird endemic to central Texas, USA. We monitored 1,382 territories in 87 patches of woodland across the breeding range from 2007 to 2011. Ours was the first evaluation of management guidelines addressing reproductive success with data collected across the warbler’s breeding range. Our results did not consistently confirm the commonly accepted management guidelines that habitat quality, based on the presence of offspring in a territory, was positively associated with patch size and territory canopy cover, and negatively associated with patch edge. The relationship between probability of a territory fledging ≥1 offspring and patch size, patch edge-to-area ratio, and territory canopy cover varied by geographic region (level-IV eco-region). Our results suggested future conservation plans that address habitat quality should consider variation among regions to improve conservation efforts and that habitat associations identified with warbler occurrence were not necessarily indicative of reproductive success.

KEY WORDS conservation, edge effect, fledging, habitat quality, patch size, Setophaga chrysoparia, songbird, territory.

For many threatened and endangered species, the amount and reliability of information about the species’ ecology at the time of listing and during development of management guidelines are often less than optimal (Tear et al. 1995). Available information is often composed primarily of anecdotal, natural-history observations, or descriptive species accounts from a few locations. Research conducted within small spatial and temporal scales provides some, but not all, of the information needed for an effective, comprehensive conservation strategy. This baseline research provides valuable information about natural history and habitat associations in particular locations, but fails to provide a comprehensive understanding of a species’ ecology throughout its geographic range (Thompson et al. 1998). Thus, not all of the necessary information is available for constructing an effective, comprehensive conservation strategy. Extrapolation and application of baseline research can result in misleading management guidelines or ineffective conservation because a species’ ecology, and thus habitat relationships, may vary across its range. Additionally, baseline research may not provide sufficient information to extrapolate to reliable assumptions about relationships between environmental conditions and habitat quality. Multiple, range-wide studies that address multiple response variables provide a more complete understanding of the ecology of a species and are necessary for developing a comprehensive conservation strategy and appropriate management guidelines.

The golden-cheeked warbler (Setophaga chrysoparia; hereafter, warbler) was listed as federally endangered in 1990 because of the perceived loss and fragmentation of its breeding habitat (USFWS 1992), woodlands of Ashe juniper (Juniperus ashei), oak (Quercus spp.), and other deciduous species in central Texas, USA (Pulich 1976, Wahl et al.
Several descriptive studies on warbler occurrence and nesting were conducted before the 1990 listing, but few studies explicitly addressed hypotheses about environmental conditions that influenced warbler occurrence and reproductive success for multiple locations across the breeding range. Research since the warbler was listed as endangered has increased knowledge about warbler occurrence (DeBoer and Diamond 2006, Magness et al. 2006, Collier et al. 2012) and nest survival (Peak 2007, Reidy et al. 2009b), but few studies have investigated relationships between reproductive success and habitat conditions that can be useful for guiding management throughout the breeding range. Furthermore, recent research has not been integrated into management guidelines (TPWD 1990, 2012; USFWS 1992). These guidelines were primarily based on warbler occurrence, which was assumed to be indicative of habitat quality, although occurrence and density were not necessarily reliable indicators of habitat quality (van Horne 1983). Management guidelines have not explicitly defined habitat quality in terms of environmental conditions relevant to survival, reproduction, and population persistence (Hall et al. 1997). Some management plans that mentioned habitat quality (SWCA 2008a, 2009; Loomis Partners Inc. 2009) cited sources that conflated occurrence and habitat quality. Consequently, assumptions about relationships between warbler reproductive success (one metric of habitat quality) and environmental conditions have been perpetuated and applied despite insufficient evidence supporting the assumed relationships and their consistency across the breeding range.

Currently, management guidelines for the warbler generally identify high-quality habitat as large patches of woodland with small patch edge-to-area ratio and dense canopy cover (TPWD 1990, 2012; USFWS 1992). These guidelines have been implemented in Habitat Conservation Plans (HCPs; SWCA 2008a, 2009; Loomis Partners Inc. 2009) and Biological Opinions (USFWS 2005). Recent HCPs have assumed that larger woodland patches provide higher quality habitat than smaller patches. The HCPs cite summaries (e.g., Ladd and Gass 1999) that refer to research that did not directly study relationships between reproductive success and patch size (Wahl et al. 1990, USFWS 1996). Some research has directly investigated relationships between reproductive success and patch size. Patch size was positively associated with reproductive success on study sites in Travis County (Coldren 1998) and within a burned area 1–3 years post-fire on Fort Hood military installation in Coryell County (Baccus et al. 2007). Additionally, warblers failed to fledge young in woodland patches ≤20 ha on private lands in Coryell County, which suggests the warbler may require a minimum patch size for reproductive success (Butcher et al. 2009). These studies examined the relationship between reproductive success and patch size in the eastern part of the breeding range; data are lacking from elsewhere in the warbler breeding range.

Management guidelines typically suggested habitat quality was negatively associated with patch edge-to-area ratio. However, the evidence for deleterious effects of edge on warbler reproductive success are unclear, perhaps in part because of challenges in disambiguating effects of patch area and patch edge (Fletcher et al. 2007). Prior to listing, studies noted the presence of warbler territories on woodland edges (Kroll 1980, Ladd 1985, Morse 1989). However, the warbler Recovery Plan (USFWS 1992:10) stated (without supporting data) that warblers “do best in large blocks of unfragmented habitat,” citing Wahl et al. (1990), who did not explicitly address edge effects. Ladd and Gass (1999) stated that warbler reproductive success was positively associated with woodland interior based on Coldren (1998), who reported results consistent with patch size effects, not edge effects, from study sites predominantly limited to Travis County. Additionally, daily survival rate of nests was negatively associated with density of forest edge within 100 m of nests on Fort Hood (Peak 2007) and was negatively associated with distance to woodland edge and density of woodland edge on study sites on Fort Hood and public lands in Travis County (Reidy et al. 2009b). Similar to patch size, studies that investigated the relationship between woodland edge and reproductive success have been restricted to the eastern part of the breeding range and are lacking elsewhere. Thus, existing data are insufficient to support the assumption of deleterious effects of edge on reproductive success of the warbler throughout its breeding range.

Management guidelines identified areas with closed-canopy Ashe juniper–oak woodland with >70% canopy cover as greater quality habitat than areas with less canopy cover (USFWS 1992; SWCA 2008a, 2009; Loomis Partners Inc. 2009). This assertion was based on the assumption that the warbler’s perceived preference for forest interior was positively associated with woodland canopy cover (Ladd and Gass 1999). Research supporting this assumption largely focused on studies of warbler occurrence on public lands in the eastern portion of the breeding range (Kroll 1980, Ladd 1985). Previous research also suggested warbler occurrence was positively associated with percent canopy cover of Ashe juniper (DeBoer and Diamond 2006); however, data linking canopy cover with reproductive success are lacking. Recent research found that warblers successfully fledged young in areas with less canopy cover than expected (as little as 20%) on public and private lands in the southwestern part of the breeding range (Klassen et al. 2012). We found little evidence in the literature that warbler reproductive success was positively associated with canopy cover and data used to support this assertion have thus far been restricted to public lands in the eastern portion of the breeding range.

Guidelines from the warbler Recovery Plan (USFWS 1992) recommend protection and management of all existing warbler habitat on public land and prioritizing conservation on nearby private lands. It is unknown whether research findings on public lands are representative or applicable to private lands, where most warbler habitat occurs (DeBoer and Diamond 2006, Collier et al. 2012). Research has predominantly been conducted on public land, particularly Fort Hood, Camp Bullis, and Balcones Canyonlands National Wildlife Refuge, even though warbler habitat on public land comprises only 4% of their breeding habitat (Groce et al. 2010). Land uses may differ between public and private land.
in the warbler’s breeding range, but it is unclear how these differences may affect relationships between reproductive success and habitat variables mentioned in management guidelines.

Although management guidelines that address reproductive success of the warbler have been applied for decades, these assumptions have not been subjected to empirical tests with data collected throughout the warbler’s breeding range. Rather than posing our own hypotheses, we evaluated existing management guidelines that address warbler reproductive success as research hypotheses. We evaluated whether the probability of a warbler territory fledging ≥1 offspring increased 1) with increasing size of woodland patches, 2) with decreasing edge-to-area ratio of patches, 3) with increasing canopy cover of territories, and 4) whether relationships in hypotheses 1–3 varied among geographic locations (eco-regions) and between public and private land.

**STUDY AREA**

We monitored warbler territories in 8 counties in the warbler’s breeding range in central Texas (Fig. 1). We monitored territories on private land in 5 counties (Bosque, Coryell, Edwards, Real, and Travis) and on public land in 6 counties (Bell, Coryell, Edwards, Kinney, Uvalde, and Travis) on Fort Hood, Barton Creek Preserve (technically privately owned, but part of a network of preserves), Garner State Park, and Kickapoo Caverns State Park. Monitored territories occurred in the 3 largest level-IV eco-regions defined by U.S. Geological Survey (Griffith et al. 2004) in the warbler’s breeding range (Fig. 1). Eco-regions are areas with similar ecosystems and environmental resources, delineated as spatial units for research and management (Griffith et al. 2004). Balcones Canyonlands was the eco-region in the southeastern portion of the Edwards Plateau, dissected by

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*Figure 1.* We monitored golden-cheeked warbler territories ($n = 1,382$) in 8 counties across the breeding range in 3 level-IV eco-regions in central Texas, USA, from 2007 to 2011.
erosion of limestone by flowing water, and had more deciduous woodland than the rest of the plateau (Griffith et al. 2004). Edwards Plateau Woodland was in the central part of the plateau and had rounded hills with woodland, whereas Limestone Cut Plain had broad valleys between mesas on Lower Cretaceous limestone (Griffith et al. 2004). We monitored warbler territories in 87 patches of oak-juniper woodland identified by Collier et al. (2012). We selected particular locations based on various needs (e.g., to study patch-size thresholds, impacts of road construction, effects of tree species composition) of each project in our research program (e.g., Butcher et al. 2009, Klassen et al. 2012); thus, we did not probabilistically sample from the breeding range.

**METHODS**

We located warbler territories by revisiting woodland patches at least once every 10 days to locate warblers as they established territories in early to mid-March. We subsequently visited each territory at least once every 10 days to delineate territorial boundaries from mid-March through May. Once we detected a warbler on a particular visit, we followed it for 30–60 minutes, recording locations with a Global Positioning System every 2 minutes or when the individual moved >20 m. While delineating territories, we also recorded breeding activity, particularly detections of fledglings, following the Vickery method of monitoring reproductive success (Vickery et al. 1992). For analyses, we considered males territorial if they were present for ≥4 weeks and territories to have fledged offspring if we detected adult warblers caring for ≥1 warbler fledgling. This approach enabled us to define territories and presence of fledglings in territories to assess management guidelines about warbler reproductive success.

We created a minimum convex polygon for each territory based on location points for each male. We used woodland patches identified by Collier et al. (2012), which used an unsupervised classification of LANDSAT 5 imagery (30-m pixel) to identify woodland. We used a suite of tools in ArcMap (version 10.0, ESRI) to calculate several metrics, including the size and edge of each woodland patch, and calculated an edge-to-area ratio of each patch. For each territory polygon, we assigned patch characteristics of either the patch it was located in or the nearest patch to the territory centroid if the territory overlapped multiple patches. Additionally, using zonal statistics, we calculated mean canopy cover for each territory using the tree-canopy density layer (Huang et al. 2001) in the U.S. Geological Survey 2001 National Landcover Dataset. We used delineations of level-IV eco-regions of the conterminous United States (Griffith et al. 2004) to assign each territory to an eco-region. Lastly, we categorized each territory as located on either publically or privately owned land.

**Analysis**

We used box-plots to visualize distribution of the data and logistic regression models to predict probability of a territory fledging ≥1 young, given predictor variables (Harrell 2001). Based on current management guidelines, models regressed fledging based on predictor variables of interest. We used 2 logistic regression models for each of the 3 predictor variables, incorporating eco-region in one set of models and public or private land ownership in the others, for a total of 6 models. We constructed each model with eco-region or land ownership as additive to the predictor variable of interest and as an interaction term to assess relationships among eco-regions and between public and private land ownership. The models were structured as: logit(fledges) = 1 + predictor + factor + predictor × factor, fledges was 1 for territories that fledged ≥1 young and 0 for territories that failed. predictor, was one of the continuous variables of interest (patch size, patch edge-to-area ratio, canopy cover of territory), factor, was either land ownership (public or private) or level-IV eco-region (Balcones Canyonlands, Edwards Plateau Woodland, or Limestone Cut Plain).

We predicted probability of fledging from each fitted model over the range of values of each predictor variable observed for each factor. We also evaluated biological significance of the direction and magnitude of effects based on ecology of the warbler (Cherry 1998, Johnson 1999). We used R 2.14.1 for all statistical analyses (R Core Development Team 2012).

**RESULTS**

We monitored 1,382 territories in 87 patches of woodland (Table 1). Fifty-one percent of territories fledged ≥1 young. Values for predictor variables largely overlapped for territories that did and did not fledge young in each eco-region (Fig. 2). The largest difference occurred in Balcones Canyonlands, where median patch size was 152% greater for territories without fledglings (757 ha) than territories with fledglings (300 ha; Fig. 2). Values for predictor variables also largely overlapped for territories with and without fledglings on private and public land (Fig. 3). The largest difference occurred on private land, where median patch size was 74% greater for territories without fledglings (402 ha) than for territories with fledglings (231 ha; Fig. 3).

Results of each logistic regression model for warbler reproductive success among eco-regions showed that patterns in Balcones Canyonlands were inconsistent with previous management guidelines (Table 2). Contrary to management guidelines, predicted probability of fledging decreased with increasing patch size in Balcones Canyonlands, whereas fledging increased with increasing patch size in Edwards Plateau Woodland and Limestone Cut Plain (Fig. 4). In patches <500 ha, the mean estimate of probability of fledging for Balcones Canyonlands was greater than and outside the confidence interval (CI) for Limestone Cut Plain. Probability of fledging increased with increasing patch edge-to-area ratio in Balcones Canyonlands and fledging decreased with increasing edge-to-area ratio in Edwards Plateau Woodland and Limestone Cut Plain (Fig. 4). The mean estimate for Balcones Canyonlands was greater than and outside of the CI for Limestone Cut Plain over the range of values for edge-to-area ratio. Contrary to management guidelines, predicted probability of fledging decreased with increasing percent canopy cover of territories in Balcones Canyonlands.
Table 1. Number of golden-cheeked warbler territories and woodland patches monitored in each level-IV eco-region on public and private land across the breeding range in central Texas, USA, from 2007 to 2011. The total number of patches is 87 rather than 89 because we monitored territories in 2 patches that exist on public and private land.

<table>
<thead>
<tr>
<th>Eco-region</th>
<th>Public Territories</th>
<th>Public Patches</th>
<th>Private Territories</th>
<th>Private Patches</th>
<th>Total Territories</th>
<th>Total Patches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balcones Canyonlands</td>
<td>301</td>
<td>8</td>
<td>195</td>
<td>16</td>
<td>496</td>
<td>24</td>
</tr>
<tr>
<td>Edwards Plateau Woodland</td>
<td>25</td>
<td>16</td>
<td>55</td>
<td>7</td>
<td>80</td>
<td>23</td>
</tr>
<tr>
<td>Limestone Cut Plain</td>
<td>701</td>
<td>32</td>
<td>105</td>
<td>10</td>
<td>806</td>
<td>42</td>
</tr>
<tr>
<td>Total</td>
<td>1,027</td>
<td>56</td>
<td>355</td>
<td>33</td>
<td>1,382</td>
<td>87</td>
</tr>
</tbody>
</table>

Canyonlands, whereas fledging increased with increasing canopy cover in Edwards Plateau Woodland and Limestone Cut Plain (Fig. 4). For canopy cover <50%, the mean estimate for Balcones Canyonlands was greater than and outside the CIs for the other eco-regions.

Results of each logistic regression model for warbler reproductive success showed the relationship was in different directions for public and private land ownership, but differences were within CIs (Table 3). Probability of fledging increased with increasing patch size for public land and decreased with increasing patch size for private land (Fig. 5). The CI for public land contained the mean estimate for private land in patches <500 ha. Probability of fledging increased with increasing edge-to-area ratio on public land and decreased with increasing edge-to-area ratio on private land (Fig. 5). The mean estimate for public land was inside the CI over the range of values for edge-to-area ratio observed on private land. Probability of fledging increased with

Figure 2. Box-plots of patch size, patch edge-to-area ratio, and percent canopy cover of territories for golden-cheeked warbler territories \((n = 1,382)\) that did and did not fledge young in each level-IV eco-region in study areas spread across the breeding range in central Texas, USA, from 2007 to 2011.
increasing percent canopy cover in territories on public land and decreased with increasing canopy cover on private land (Fig. 5). The mean estimates for public and private lands were within CIs of each other over the range of canopy cover.

**DISCUSSION**

Overall, we did not find consistent relationships between reproductive success and 1) patch size, 2) patch edge-to-area ratio, and 3) percent canopy cover in territories for golden-cheeked warbler territories across the breeding range in central Texas, USA, from 2007 to 2011.

**Table 2.** Results of 3 logistic regression models for predicting fledging success of golden-cheeked warbler territories from 2007 to 2011 for each predictor variable (patch size, patch edge-to-area ratio, and percent canopy cover in territory) by level-IV eco-regions across the warbler’s breeding range in central Texas, USA.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Intercept</td>
<td>0.3923</td>
<td>0.1217</td>
<td>0.0013</td>
</tr>
<tr>
<td></td>
<td>Patch size (ha)</td>
<td>−0.0001</td>
<td>0.0001</td>
<td>0.1478</td>
</tr>
<tr>
<td></td>
<td>Eco-region, Edward Plateau Woodland</td>
<td>−0.6411</td>
<td>0.3345</td>
<td>0.0553</td>
</tr>
<tr>
<td></td>
<td>Eco-region, Limestone Cut Plain</td>
<td>−0.5574</td>
<td>0.1647</td>
<td>0.0007</td>
</tr>
<tr>
<td></td>
<td>Patch size × Edwards Plateau Woodland</td>
<td>0.0007</td>
<td>0.0010</td>
<td>0.4156</td>
</tr>
<tr>
<td></td>
<td>Patch size × Limestone Cut Plain</td>
<td>0.0003</td>
<td>0.0002</td>
<td>0.0697</td>
</tr>
<tr>
<td>2</td>
<td>Intercept</td>
<td>−0.0146</td>
<td>0.3014</td>
<td>0.9613</td>
</tr>
<tr>
<td></td>
<td>Edge-to-area ratio (m/ha)</td>
<td>0.0024</td>
<td>0.0024</td>
<td>0.3134</td>
</tr>
<tr>
<td></td>
<td>Eco-region, Edward Plateau Woodland</td>
<td>1.0731</td>
<td>0.8264</td>
<td>0.1941</td>
</tr>
<tr>
<td></td>
<td>Eco-region, Limestone Cut Plain</td>
<td>0.1028</td>
<td>0.3676</td>
<td>0.7797</td>
</tr>
<tr>
<td></td>
<td>Edge-to-area ratio × Edward Plateau Woodland</td>
<td>−0.0077</td>
<td>0.0042</td>
<td>0.0644</td>
</tr>
<tr>
<td></td>
<td>Edge-to-area ratio × Limestone Cut Plain</td>
<td>−0.0039</td>
<td>0.0031</td>
<td>0.2107</td>
</tr>
<tr>
<td>3</td>
<td>Intercept</td>
<td>0.7766</td>
<td>0.4339</td>
<td>0.0735</td>
</tr>
<tr>
<td></td>
<td>Canopy cover (%)</td>
<td>−0.0065</td>
<td>0.0057</td>
<td>0.2585</td>
</tr>
<tr>
<td></td>
<td>Eco-region, Edward Plateau Woodland</td>
<td>−1.1898</td>
<td>0.7501</td>
<td>0.1127</td>
</tr>
<tr>
<td></td>
<td>Eco-region, Limestone Cut Plain</td>
<td>−2.3731</td>
<td>0.7931</td>
<td>0.0028</td>
</tr>
<tr>
<td></td>
<td>Canopy cover × Edwards Plateau Woodland</td>
<td>0.0142</td>
<td>0.0151</td>
<td>0.3482</td>
</tr>
<tr>
<td></td>
<td>Canopy cover × Limestone Cut Plain</td>
<td>0.0261</td>
<td>0.0099</td>
<td>0.0085</td>
</tr>
</tbody>
</table>
ratio, and 3) canopy cover in territories across the breeding range of the warbler. Similarly, we did not find consistent relationships between reproductive success and predictor variables when comparing public and private land. We found larger differences between predictor variables and reproductive success among eco-regions than between public and private land ownership, which suggests that conservation of the warbler might benefit from management guidelines.

Table 3. Results of 3 logistic regression models for predicting fledging success of golden-cheeked warbler territories (n = 1,382) from 2007 to 2011 for each predictor variable (patch size, patch edge-to-area ratio, and percent canopy cover in territory) by public and private land across the warbler's breeding range in central Texas, USA.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Intercept</td>
<td>0.2210</td>
<td>0.1608</td>
<td>0.1695</td>
</tr>
<tr>
<td></td>
<td>Patch size (ha)</td>
<td>-0.0006</td>
<td>0.0003</td>
<td>0.0654</td>
</tr>
<tr>
<td></td>
<td>Land, public</td>
<td>-0.1756</td>
<td>0.1835</td>
<td>0.3387</td>
</tr>
<tr>
<td></td>
<td>Patch size × land, public</td>
<td>0.0006</td>
<td>0.0003</td>
<td>0.0549</td>
</tr>
<tr>
<td>2</td>
<td>Intercept</td>
<td>0.4677</td>
<td>0.3807</td>
<td>0.2190</td>
</tr>
<tr>
<td></td>
<td>Edge-to-area ratio (m/ha)</td>
<td>-0.0033</td>
<td>0.0026</td>
<td>0.1960</td>
</tr>
<tr>
<td></td>
<td>Land, public</td>
<td>-0.4526</td>
<td>0.4099</td>
<td>0.2700</td>
</tr>
<tr>
<td></td>
<td>Edge-to-area ratio × land, public</td>
<td>0.0039</td>
<td>0.0029</td>
<td>0.1720</td>
</tr>
<tr>
<td>3</td>
<td>Intercept</td>
<td>0.2669</td>
<td>0.3771</td>
<td>0.4790</td>
</tr>
<tr>
<td></td>
<td>Canopy cover (%)</td>
<td>-0.0034</td>
<td>0.0056</td>
<td>0.5420</td>
</tr>
<tr>
<td></td>
<td>Land, public</td>
<td>-0.5121</td>
<td>0.5631</td>
<td>0.3630</td>
</tr>
<tr>
<td></td>
<td>Canopy cover × land, public</td>
<td>0.0080</td>
<td>0.0076</td>
<td>0.2930</td>
</tr>
</tbody>
</table>
particular to geographic location in the breeding range. Our results from territories monitored throughout the warbler’s breeding range do not consistently support current management guidelines addressing reproductive success.

Eco-Region
A positive association between reproductive success and patch size has been shown to occur locally in the eastern portion of the warbler’s breeding range (Coldren 1998, Baccus et al. 2007); however, we found the relationship depended on eco-region. We found little evidence of a consistent association across the breeding range of the warbler as previously suggested in management guidelines (SWCA 2008b, 2009; Loomis Partners Inc. 2009). In fact, we found the direction of the relationship between reproductive success and patch size to be negative in Balcones Canyonlands.

The relationship between reproductive success and patch size, patch edge-to-area ratio, and percent canopy cover in a territory on public and private land based on data collected across the breeding range in central Texas, USA, from 2007 to 2011. Dashed lines show 95% confidence intervals.

![Figure 5](image-url)

Figure 5. Predicted probability of a golden-cheeked warbler fledging ≥1 offspring in a territory given patch size, patch edge-to-area ratio, and percent canopy cover in a territory on public and private land based on data collected across the breeding range in central Texas, USA, from 2007 to 2011. Dashed lines show 95% confidence intervals.

Relationships between reproductive success and patch edge-to-area ratio also varied by eco-region, and the relationship was not always negative as previously assumed in management guidelines. We found the direction of the relationship between reproductive success and patch edge-to-area ratio was positive in the Balcones Canyonlands eco-region, which is inconsistent with previous findings for nests monitored at Fort Hood (Peak 2007) in the Limestone Cut Plain eco-region. Our results for edge-to-area ratio are likely unsurprising to researchers because factors that influence reproductive success that may be associated with patch edge, such as nest predator assemblages and food availability (Chalfoun et al. 2002, Sperry and Taylor 2008), may vary over broad geographic extents, leading to different regional, ecological interactions between reproductive success and patch edge.

The relationship between reproductive success and canopy cover also depended on the geographic location in the warbler breeding range. We found the direction of the relationship between reproductive success and canopy cover was negative in Balcones Canyonlands, which was inconsistent with previous management guidelines (Loomis Partners Inc. 2009, SWCA 2009, TPWD 2012). Warbler occurrence has been shown to be positively associated with percent canopy cover of Ashe juniper (DeBoer and Diamond 2006), and management guidelines assumed that reproductive success was positively associated with occurrence of the warbler. However, ecological factors affecting occupancy should not necessarily be assumed to have the same relationship with reproductive success. Percent canopy cover may influence presence of the warbler in particular locations, but other factors, including predation of nests (Stake et al. 2004), nesting females (Reidy et al. 2009a), and fledglings, may
be more influential on reproductive success or other metrics of habitat quality.

Until recently, previously published research on warblers had not examined the potential importance of regional differences in habitat characteristics for reproductive success. Klassen et al. (2012) found that warblers occupied and successfully reproduced in areas with as little as 20% canopy cover in the southwestern part of the breeding range. Management guidelines (TPWD 2012) indicated that areas with <35% canopy cover were not habitat and therefore were presumably unsuitable for reproduction. Our, and recent, results suggest regional variation in habitat relationships should be considered when defining warbler habitat and for understanding habitat quality to improve conservation efforts.

Public and Private Land
We did not find large differences in relationships between reproductive success and predictor variables on public versus private land. The direction of the relationship was different between public and private land for each predictor variable; however, 95% CIs largely overlapped over the range of each predictor variable. As with eco-region, we did not find a consistent direction of the relationship between reproductive success and patch size, edge-to-area ratio, and canopy cover. Although land use may vary between public and private land, the relationship between warbler reproductive success and predictor variables may not be different because different land uses may not change these relationships.

Summary
Although our results may be surprising to some readers familiar with management prescriptions for the warbler, ours was the first evaluation of assumed relationships between reproductive success and habitat variables across the warbler’s breeding range. We treated current management guidelines as hypotheses that can and should be evaluated with, and potentially revised based on, data collected across the breeding range. Data may have been previously unavailable or insufficient to evaluate assumed relationships between reproductive success and predictor variables. Although we collected a large dataset across the warbler’s breeding range, we do not suggest our results definitively dictate management guidelines for reproductive success. Rather, we consider this analysis as one of many contributions to understanding the warbler’s ecology to further its conservation.

MANAGEMENT IMPLICATIONS
Application of results from a few locations may misguide conservation strategies applied to the range of a species. Although probability of warbler occupancy has been shown to be positively associated with patch size of woodlands (Collier et al. 2012), one should not assume that patch size was important for reproductive success. In the case of the breeding range of the warbler, prioritizing conservation in locations based on large patch size, less patch edge-to-area ratio, and greater canopy cover do not appear to provide consistently greater reproductive success and might overlook other conditions that provide successful breeding opportunities for the warbler. Current management guidelines focused on conserving large woodland patches may not provide better reproductive success to the warbler depending on the particular geographic location in the breeding range. Management guidelines may need to be specific to each eco-region depending on relationships between reproductive success and habitat characteristics in each region. Additionally, a strategy focused on conservation of large patches of oak–juniper woodland might unnecessarily exclude lands containing smaller patches that do not necessarily have lesser reproductive success. In a private–land state such as Texas, a successful conservation strategy should engage as many landowners as possible whose contributions can aid conservation of the warbler.

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