Influence of the spatial pattern of conserved lands on the persistence of a large population of red-cockaded woodpeckers

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Abstract

Spatial configuration of habitats can affect chances of survival for many rare species, especially those with low dispersal rates or large area requirements. The red-cockaded woodpecker (Picoides borealis) disperses relatively short distances and also requires large blocks of habitat — characteristics that make its populations especially sensitive to the distribution of its habitat across a region. We created conservation scenarios for a large population of red-cockaded woodpeckers based on acquisition of conservation easements on different properties, and we then estimated the probability of long-term persistence using Geographic Information System technology and a stochastic demographic model. We considered four broad conservation scenarios: (1) conservation of only those properties that currently have easements (Status quo); (2) random acquisition of additional conservation properties (Random); (3) strategic acquisition of additional conservation properties (Strategic); and (4) all properties that have red-cockaded woodpeckers gain protection (Total Protection). The data used in the analyses come from the sixth-largest population (ca. 180 groups), which occurs exclusively on private lands in the Red Hills region of north Florida and south Georgia. Chances of survival exclusively on existing easements were low unless large-scale improvements in habitat quality were realized. Easements acquired in random order also did not effectively conserve the large aggregations of active territories important to population persistence. Even when up to 20,000 ha of new easements were added randomly, densities and distributions of active territories generally remained critically over-dispersed. Random acquisition of easements did not approximate the additions of habitat based on biological criteria until 30,000 ha were added and an average of 60% of all clusters was conserved, and even then neighborhood sizes were roughly half the sizes of neighborhoods produced using biological criteria. Alternatively, use of biological criteria to select key properties with a total area < 10,000 ha better approximated several spatial characteristics associated with population persistence. Overall, scenarios that provided the highest likelihood of long-term survival conserved core properties and expanded the population on existing easements through habitat improvement and intensive management techniques. This will require ca. 17,000 ha in new easements. We also suggest that management be used to augment populations on existing easements, particularly peripheral regions where populations of ca. 25 territories might eventually be established. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Red-cockaded woodpecker; Private lands; Spatially explicit model; Population persistence; Red Hills; Cluster activity; Ecological neighborhoods

1. Introduction

Recent research on spatial ecology (e.g. Kareiva and Wennergren, 1995; Tilman and Kareiva, 1997) has led biologists to consider many new variables in their attempts to conserve rare species. Habitat availability is of course a dominant concern (Simberloff, 1988; Fahrig, 1997), but the size, shape, and distribution of habitat patches across a region, and the influence that such spatial distributions might have on population persistence, are increasingly recognized at the outset of many conservation efforts. Indeed, conservation efforts that do not consider such variables have faced increasing criticism (Pulliam et al., 1992; Arnold et al., 1993; Harrison, 1993; Dunning et al., 1995; Wahlberg et al., 1996; Huxel and Hastings, 1999).

Property ownership boundaries are a potentially important feature that could affect the size, shape, and configuration of patches of habitat that might be conserved. Property ownership patterns have been shown to influence the spatial heterogeneity of regions (Crow et al., 1999), but, based on a review of 230 recent articles where spatial features were measured, relatively few investigations (Maehr and Cox, 1995; Wigley and...

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Sweeney, 1995; Crow et al., 1999) have considered property ownership boundaries as a variable of interest. This may stem from the difficulty of processing property ownership information, but the conservation of many rare species requires a focus on private lands (Bean and Wilcove, 1997), so the distribution of property ownerships often represents a key feature to consider.

We considered how different spatial configurations of property ownerships might fragment habitat for and influence the long-term persistence of a large population of red-cockaded woodpeckers (Picoides borealis). The red-cockaded woodpecker is an endangered species that occupies old-growth pine forests of the southeastern United States (Lennartz and Henry, 1985). Individuals use cavities excavated in mature (100+ years), living pine trees. Site occupancy is influenced by habitat conditions immediately surrounding the cluster of cavity trees (hereinafter “cluster”) that make up territory centers (Hooper et al., 1980; Walters, 1990) as well as by features extending over a much larger area (Conner and Rudolph, 1991; Thomlinsen, 1995; Engstrom and Mikusinski, 1998; Cox et al., unpub. data). For example, “active” clusters (occupied by woodpeckers) tend to be surrounded by more active clusters than “inactive” clusters (Conner and Rudolph, 1991; Thomlinsen, 1995; Cox et al., unpub. data). A spatially explicit population model for red-cockaded woodpeckers (Letcher et al., 1998) also has shown that, given the low frequency of dispersal >5 km (Walters et al., 1988), population persistence is closely linked to the dispersion of territories over a region. A broad dispersion of active clusters has also been adduced as a possible reason for some population declines (Beyer et al., 1996; Engstrom and Mikusinski, 1998). The long-term persistence of woodpecker populations, thus, should be sensitive to habitat changes occurring beyond the boundaries of individual properties.

The potential influence of the surrounding landscape on red-cockaded woodpecker persistence is consistent with recent theoretical investigations of population survival in fragmented landscapes using spatially explicit models (Tilman et al., 1994; Huxel and Hastings, 1999). These modeling studies predict that sedentary species like the red-cockaded woodpecker should become extinct more rapidly in fragmented landscapes. We examined the influence of population fragmentation using the distribution of property ownerships and red-cockaded woodpeckers in the Red Hills physiographic region of north Florida and southwest Georgia, which is the sixth largest woodpecker population remaining (James, 1995; 3.8% of the total) and the largest population on private lands. We use these analyses to examine how property ownerships might affect habitat fragmentation and woodpecker survival, and to establish conservation priorities. This has practical importance for the Red Hills Conservation Program (Anon., 1996), which is attempting to conserve habitat for this population using conservation easements and habitat management techniques.

Our objective was to analyze the influence of the spatial arrangement of conserved properties on the survival potential of the Red Hills population of red-cockaded woodpeckers. Our approach consisted of developing conservation scenarios using existing ownership boundaries and then evaluating resulting changes in habitat distribution, population persistence (as measured using a stochastic demographic model), and other population metrics.

2. Study area and methods

The Red Hills physiographic region covers an estimated 4274 km² of north Florida and south Georgia (Fig. 1). The boundaries of the region are defined by the Ochlockonee and Aucilla rivers and the Cody escarpment. The southern portion of the Red Hills is dominated by Tallahassee, Florida, with a population of 300,000 people, and the northern portion is dominated by Thomasville, Georgia, with a population of 16,000 people. The Red Hills population of red-cockaded woodpeckers consists of ca. 180 active and 70 inactive clusters (Engstrom and Baker, 1995; Cox et al., unpub. data). A more complete description of the region is provided in Engstrom and Baker (1995).

Field surveys were conducted from February–June 1999. Clusters of cavity trees identified in Baker (1982) and Engstrom and Baker (1995) were visited to ascertain the current status of each cluster. Activity of individual trees was assessed using procedures described by Jackson (1977) and Hooper et al. (1980). Additional surveys of potentially suitable habitat were made as time permitted, usually by vehicle.

Locations of >2000 active and inactive cavity trees (Jackson, 1977) were georeferenced using a Trimble GeoExplorer II unit (Trimble Navigation Limited, 645 North Mary Avenue, Sunnyvale, CA). A minimum of 45 positions was recorded at each cavity tree. Positions were then processed using differential correction procedures (Trimble Navigation Limited, 1997). The estimated twodimensional variation of corrected positions was in the order of 1–2.5 m.

Property boundaries (Fig. 1) and other habitat features were processed using aerial photography and other ArcInfo, ArcView (Environmental Systems Research Institute, Inc., 380 New York Street, Redmond CA), or RAMAS (Akçakaya and Root, 1998) software. Ownership information and parcel boundaries were taken from county tax records processed in 1997. The boundaries for single parcels >100 ha (n = 104) were transcribed to 1:7200 aerial photographs for digitizing. These large private ownerships (Fig. 1) cover 1272 km². The 10 largest ownerships encompass 28% of the total area, while 19 of the largest ownerships make up about half the total area.
Lakes and ponds, forested uplands and wetlands, and fields and urban areas also were digitized from 1:7200 aerial photographs. All geographic data were processed for GIS analysis using a Universal Transverse Mercator projection (Zone 16, North American datum 1983).

2.1. Red-cockaded woodpecker conservation scenarios

In the first group of scenarios (subheading Status quo in Table 1), we considered the response of the red-cockaded woodpecker population in the Red Hills if no additional properties were conserved. We make the assumption that habitat on all other private lands will eventually be lost, and woodpeckers will be restricted to the properties currently protected. At the other extreme we constructed the Total Protection scenario, in which all properties containing active and inactive clusters were conserved.

Other conservation scenarios were subdivided into Random and Strategic scenarios (Table 1). Easements and other forms of deed restrictions currently exist for 23 parcels that encompass 27,700 ha in the Red Hills (Fig. 1). Random scenarios were created by sampling random suites of properties that totaled ca. 10,000 (Random 1), 20,000 (Random 2), and 30,000 ha (Random 3). New easements have been secured at a rate of ca. 1000–2000 ha (1–4 properties) per year over the past 8 years (Anon., 1996), so conservation of an additional 10,000–20,000 ha over the next 10 years (Random 1 and Random 2, Fig. 1).
Table 1

Conservation scenarios considered for the Red Hills population of red-cockaded woodpeckers

<table>
<thead>
<tr>
<th>Scenarios</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Status quo</td>
<td>No additional easements</td>
</tr>
<tr>
<td>Occupied Habitat</td>
<td>Includes occupied habitat within existing easements and lands with other types of long-term protection; easements with red-cockaded woodpeckers encompass 10,580 ha.</td>
</tr>
<tr>
<td>Potential Habitat</td>
<td>Includes all upland habitat within existing easements and lands with other types of long-term protection; assumes habitat management and restoration can expand the population significantly.</td>
</tr>
<tr>
<td>Random</td>
<td></td>
</tr>
<tr>
<td>Random 1, 2, and 3</td>
<td>Unprotected properties were selected randomly without replacement until 10,000, 20,000, and 30,000 ha were added to existing easements. For each of the three totals (Random 1, Random 2, and Random 3), 10 random samples were taken.</td>
</tr>
<tr>
<td>Strategic–Population Based</td>
<td></td>
</tr>
<tr>
<td>Small Populations</td>
<td>Properties with &lt;10 clusters were isolated; this scenario involved 23 new properties with a total area of 31,720 ha.</td>
</tr>
<tr>
<td>Medium Populations</td>
<td>Properties containing &gt;10 clusters were isolated; this scenario included large properties (see below) and involved 13 new properties with a total area of 13,820 ha and includes four properties that satisfied conditions for the Large Populations scenario.</td>
</tr>
<tr>
<td>Large Populations</td>
<td>Properties with &gt;18 clusters were isolated; this scenario involved four new properties with a total area of 6,322 ha.</td>
</tr>
<tr>
<td>No Peripheral Populations</td>
<td>New easements limited to the single largest neighborhood (polygon A, Fig. 3) identified using existing habitat conditions; this scenario involved existing easements and 23 new properties that had a total area of 24,379 ha.</td>
</tr>
<tr>
<td>Core Populations</td>
<td>Easements limited to two large properties with &gt;15 clusters and located between two existing easements with large woodpecker populations (Sites A and B, Fig. 3); this scenario involved 2,978 ha.</td>
</tr>
<tr>
<td>Strategic–Expert Opinion Based</td>
<td></td>
</tr>
<tr>
<td>Highest Overall Score</td>
<td>Properties with an overall priority score &gt;3 (Anon., 1996) were isolated; involved 12 new properties with a total area of 28,126 ha.</td>
</tr>
<tr>
<td>Highest Upland Scores</td>
<td>Properties with upland scores &gt;3 (Anon., 1996) were isolated; involved 14 new properties with a total area of 24,842 ha.</td>
</tr>
<tr>
<td>Highest Connectivity Scores</td>
<td>Properties with connectivity scores &gt;3 (Anon., 1996) were isolated; involved 14 new properties with a total area of 25,326 ha.</td>
</tr>
<tr>
<td>Total Protection</td>
<td>Includes all properties with red-cockaded woodpecker clusters; involved 31 properties and 41,595 additional ha.</td>
</tr>
</tbody>
</table>

*Italicized phrases under the heading Scenarios are used in the text.

respectively) represents a reasonable estimate of the rate of growth of conserved lands. Random 3 (the addition of 30,000 ha to the current base of conserved lands) corresponds to a more ambitious, long-term goal of conserving a total of 60,000 ha within the region. These Random scenarios reflected the manner in which easements have been obtained and also provided null models for comparisons with Strategic scenarios.

Ideally, targeting properties for conservation easements should be based on biological considerations (e.g. the distribution of woodpecker clusters). The scenarios taking such approaches were termed Strategic (Table 1). Strategic scenarios based on the number or arrangement of woodpecker clusters were termed Population-Based scenarios, while the Expert Opinion scenarios were based on a scoring system developed for each property by staff in the Red Hills Conservation Program (Anon., 1996). The overall Expert Opinion score (Anon., 1996) was based on six variables: (1) quality of upland habitats; (2) quality of wetland habitats; (3) extent of development; (4) scenic quality; (5) threat posed; and (6) connectivity. Properties with high-ranking scores in two of these categories (Highest Upland Scores and Highest Connectivity Scores) also were considered separately.

2.2. Neighborhood and habitat characteristics

For each conservation scenario (Table 1), we isolated the woodpecker clusters within the properties identified and computed the total number of active clusters, the number of active clusters in regional neighborhoods defined by a 2 km search radius, the number of active neighbors within a 2 km radius of each cluster, and other features that might influence population stability and cluster activity (Conner and Rudolph, 1991; Thomlinson, 1995; Cox et al., unpub. data). The distance of 2 km was based on analyses of cluster activity in this population (Cox et al., unpub. data) and others (Conner and Rudolph, 1991; Thomlinson, 1995), the estimated distances of frequent dispersal events (Walters et al., 1988; Walters, 1990), and characteristics of ecological neighborhoods throughout the range of this species (Engstrom and Mikusinski, 1998). We estimated the location of cluster centers (median x-, y-coordinates of cavity trees in the cluster; Lipscomb and Williams, 1995) to include or exclude clusters by property boundaries and to estimate the number of active clusters within 2 km. As noted, the number of active clusters within 2 km is highly correlated with cluster activity and
hence population stability (Conner and Rudolph, 1991; Thomlinson, 1995; Cox et al., unpub. data).

To assess changes in habitat patch characteristics created by different scenarios, we drew a circle with a radius of 804 m around each cluster center. This distance has been used to delineate red-cockaded woodpecker management areas surrounding individual clusters (Costa, 1992; Lipscomb and Williams, 1995), and within this area we eliminated unsuitable habitat types (i.e., lakes, fields, and forested wetlands) and created a layer consisting exclusively of the upland forest lands surrounding the cluster. This layer was then converted to a raster layer (required by RAMAS GIS and analytical tools such as Rempel et al., 1999) using a minimum cell size of 30 m². Population sizes (used to initiate stochastic models in RAMAS Metapop) were calculated by dividing the total area of habitat available within each property by 120. This divisor gave numbers of active and inactive clusters similar to those observed in the field. The habitat cells created using these procedures are referred to as “near-cluster habitat”.

We defined neighborhoods as patches of near-cluster habitat that occurred within 2 km of one another. A neighborhood represents a heterogenous feature (a group of grid cells) within which spatial interactions among individuals were presumed to be frequent (Fahrig, 1988). The distance of 2 km was based again on observed dispersal distances and other information (Hooper et al., 1982; Walters, 1990; Conner and Rudolph, 1991; Hooper and Lennartz, 1995; Engstrom and Mikusinski, 1998).

Construction of artificial cavities (Copey et al., 1991) has been used to expand populations quickly in some areas, including the Red Hills (Carter et al., 1995); therefore, we considered another scenario (Status quo—Potential Habitat) where potential habitat within easements was not as closely linked to cavity trees. In this scenario, which was designed to assess the potential effectiveness of management within existing easements, all the upland forests within existing easements were converted to a raster layer with a minimum cell size of 30 m².

Procedures used to define patches of habitat and neighborhoods were run independently for each scenario, and landscape metrics (e.g., fractal dimension, area/edge ratios, total area, number of neighborhoods, etc.) were calculated using analytical programs designed for ArcView (e.g., McGarigal and Marks, 1993; Rempel et al., 1999) or RAMAS GIS (Akçakaya and Root, 1998) software. Inter-patch measurements were based on the nearest edge-to-edge distance.

2.3. Population model

Population simulations were performed using RAMAS Metapop (Akçakaya and Root, 1998). RAMAS Metapop is a stochastic, stage-structured model that tracks groups of semi-isolated neighborhoods through time. Individuals move among neighborhoods based on a dispersal function (Akçakaya and Root, 1998). Since RAMAS is a generalized population model that does not incorporate the social structure evident in red-cockaded woodpecker populations (Walters, 1990), we made several simplifying assumptions (Appendix A). Heppel et al. (1994) presented a simplified male-based population model to analyze different management strategies for red-cockaded woodpeckers, but we elected to use a female-based model because female life-history traits more closely matched parameters in RAMAS Metapop (Appendix A).

The female-based model had four stages (Appendix A) that corresponded to distinctive portions of the female life cycle. Specific survival and fecundity parameters (Appendix A) were derived from Stevens (1995) with some minor adjustments based on data presented in Lennartz et al. (1987) and Reed et al. (1988). Demographic parameters in Stevens (1995) were estimated from a “stable” population in central Georgia consisting of 34 active groups. These parameters produced an expanding population (lambda = 1.0039) that, based on an elasticity analysis (Caswell, 1989), was most sensitive to the survival and fecundity parameters in Stages 1 and 4 (Appendix A). Since the demographic parameters produced a positive growth rate, persistence times were influenced most by environmental and demographic stochasticity, the geographic structure of populations, and the carrying capacity of patches of habitat. Additional aspects of the model are provided in Appendix A.

Simulations were carried out for 100 years, and a total of 500 simulations was performed for each scenario considered. The primary measure used to compare results from different scenarios was the probability of quasi-extinction at the end of a 100-year simulation (Akçakaya and Root, 1998). Descriptive statistics, Pearson correlation coefficients, and other statistical comparisons were performed using Systat (Wilkinson, 1998). The Kolmogorov–Smirnov test statistic, D, also was used to compare extinction risk curves (Akçakaya and Root, 1998) generated by the different conservation scenarios, particularly those with similar terminal quasi-extinction probabilities (Ginzberg et al., 1990). This statistic helped to discern important differences not evident in the terminal quasi-extinction probabilities (Ginzberg et al., 1990).

3. Results

Under the worst-case scenario where the Red Hills population of red-cockaded woodpeckers was restricted to existing easements (Status quo—Occupied Habitat scenario), total population size decreased from 180 to 30 active clusters in 100 year projections. Clusters supported
under this worst-case scenario were distributed among five small, isolated neighborhoods, the largest of which contained <20 active clusters (Table 2). Four of five neighborhoods remaining under this scenario contained <3 active clusters, while the mean distance to the nearest active neighbor decreased from the current average of 636 m (Total Protection scenario) to 3141 m, and the number of active neighbors within 2 km decreased from an average of 8.6 to 3.9.

As new conservation easements were added randomly to the existing easements (Random 1, Random 2, and Random 3), population and neighborhood sizes moved somewhat closer to values estimated for the best-case scenario (Total Protection), but several important metrics did not change significantly (Table 2). The addition of 10,000–20,000 ha of new easements (Random 1 and 2) increased the number of protected clusters by about 30–60% compared to the worst-case scenario of Status quo (Table 2), but random easements produced widely dispersed, isolated aggregations with low surrounding densities of active clusters. The average number of active neighbors found within 2 km under random scenarios ($\mu$'s = 4.0, 5.2, and 7.4) did not differ significantly (Bonferroni-adjusted $P < 0.05$, one-sided t-test) from the worst-case scenario of no new easements ($\mu$ = 3.9) until 30,000 ha of new easements had been added. The Strategic and Random 3 (30,000 ha conserving randomly) scenarios conserved 60–70% of the active clusters in the Red Hills (Table 2) and provided neighborhood characteristics that closely mirrored those that resulted from the best-case scenario of Total Protection (Table 2). The numbers of active clusters within 2 km for Strategic and Random 3 scenarios were similar to the region-wide average of 8.6, and the number of active clusters in the largest neighborhood typically was at least four times as large as the number of active clusters in the second largest neighbor (i.e. active clusters were better aggregated).

There were, however, vast differences in the area of new easements required by these scenarios. Whereas the Random 3 scenario involved 30,000 ha of new easements, two Strategic scenarios (Core Population and Large Populations) required <8000 ha.

Notable differences existed in the neighborhood characteristics created among Strategic and Random 3 scenarios. One of the 10 Random 3 trials performed produced neighborhood characteristics nearly identical to the worst-case scenario of no additional habitat conservation. This could be taken to infer that there is about a 10% chance of no increase in population security even when very large random increases of conservation easements occurred. Similarly, the Strategic scenario involving Small Populations (<10 active clusters) required a large area of new easements but did not dramatically improve the average number of active clusters within 2 km in comparison to the worst-case scenario (Status quo—Occupied Habitat). The average for the worst-case scenario was 3.9, while the average under the Small Populations scenario was 5.6.

Table 2
Comparisons of population sizes and neighborhood and habitat characteristics for the Red Hills population of red-cockaded woodpeckers under different habitat conservation scenarios (Table 1)\(^a\)

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Total Active N</th>
<th>Active N in largest neigh.</th>
<th>Active N in 2nd largest neigh.</th>
<th>Total active N &lt; 2 km</th>
<th>Active N &lt; 1.5 km</th>
<th>Fractal dimension</th>
<th>Shape index</th>
<th>Distance (m) to nearest active</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Status quo</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occupied habitat</td>
<td>26</td>
<td>17</td>
<td>5</td>
<td>5</td>
<td>3.9</td>
<td>1.15</td>
<td>3.33</td>
<td>3141</td>
</tr>
<tr>
<td><strong>Random easements</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random 1</td>
<td>38.5 (11.6)</td>
<td>26.0 (10.6)</td>
<td>10.4 (3.1)</td>
<td>6.7 (1.2)</td>
<td>4.0 (1.8)</td>
<td>1.16 (0.01)</td>
<td>3.66 (0.44)</td>
<td>1926 (734)</td>
</tr>
<tr>
<td>Random 2</td>
<td>59.2 (18.7)</td>
<td>25.5 (11.4)</td>
<td>14.5 (9.7)</td>
<td>7.7 (0.5)</td>
<td>5.2 (2.0)</td>
<td>1.17 (0.01)</td>
<td>4.26 (0.57)</td>
<td>1544 (389)</td>
</tr>
<tr>
<td>Random 3</td>
<td>74.5 (16.5)</td>
<td>41.5 (9.8)</td>
<td>16.2 (7.6)</td>
<td>7.0 (0.8)</td>
<td>7.4 (1.6)</td>
<td>1.17 (0.01)</td>
<td>4.25 (0.40)</td>
<td>1425 (474)</td>
</tr>
<tr>
<td><strong>Strategic scenarios</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Expert opinion overall</td>
<td>117.0 (9.5)</td>
<td>92.3 (10.9)</td>
<td>17.7 (3.8)</td>
<td>5.7 (0.6)</td>
<td>12.6 (1.2)</td>
<td>1.17 (0.06)</td>
<td>5.41 (0.67)</td>
<td>1692 (464)</td>
</tr>
<tr>
<td>Highest overall scores</td>
<td>111</td>
<td>86</td>
<td>24</td>
<td>6</td>
<td>12.3</td>
<td>1.16</td>
<td>6.12</td>
<td>2382</td>
</tr>
<tr>
<td>Highest connectivity scores</td>
<td>112</td>
<td>86</td>
<td>22</td>
<td>6</td>
<td>14.0</td>
<td>1.17</td>
<td>4.78</td>
<td>2515</td>
</tr>
<tr>
<td>Highest upland scores</td>
<td>128</td>
<td>105</td>
<td>19</td>
<td>5</td>
<td>11.6</td>
<td>1.17</td>
<td>5.32</td>
<td>2091</td>
</tr>
<tr>
<td>Population based overall</td>
<td>1054.4 (37.0)</td>
<td>78.0 (48.7)</td>
<td>11.2 (8.7)</td>
<td>9.4 (4.3)</td>
<td>9.0 (2.7)</td>
<td>1.19 (0.03)</td>
<td>5.96 (1.08)</td>
<td>1521 (294)</td>
</tr>
<tr>
<td>Small populations</td>
<td>88</td>
<td>31</td>
<td>21</td>
<td>9</td>
<td>5.6</td>
<td>1.21</td>
<td>6.87</td>
<td>1348</td>
</tr>
<tr>
<td>Medium populations</td>
<td>118</td>
<td>83</td>
<td>24</td>
<td>6</td>
<td>13.1</td>
<td>1.19</td>
<td>7.23</td>
<td>1758</td>
</tr>
<tr>
<td>Large populations</td>
<td>95</td>
<td>58</td>
<td>26</td>
<td>7</td>
<td>9.5</td>
<td>1.19</td>
<td>5.43</td>
<td>2393</td>
</tr>
<tr>
<td>Core populations</td>
<td>64</td>
<td>58</td>
<td>9</td>
<td>5</td>
<td>8.0</td>
<td>1.18</td>
<td>4.61</td>
<td>2336</td>
</tr>
<tr>
<td>No peripheral</td>
<td>162</td>
<td>159</td>
<td>2</td>
<td>3</td>
<td>9.0</td>
<td>1.19</td>
<td>5.67</td>
<td>1985</td>
</tr>
<tr>
<td><strong>Total protection</strong></td>
<td>177</td>
<td>159</td>
<td>13</td>
<td>6</td>
<td>8.6</td>
<td>1.23</td>
<td>9.42</td>
<td>636</td>
</tr>
</tbody>
</table>

\(^a\) N refers to the number of active clusters. Neighborhoods (abbreviated as Neigh.) were defined using a 2 km radius and edge-to-edge distance estimates (see text). Fractal dimensions and shape indices were the average, area-weighted values for the region and were calculated using Rempel et al. (1999). Standard deviations are shown in parentheses, where appropriate.
Boundaries of neighborhoods estimated under the best-case scenario (Total Protection) suggested the Red Hills population has eight distinctive groups (Fig. 2). The large, central neighborhood (Fig. 2, polygon A) consists of 215 cavity tree clusters (86% of total active and inactive clusters in the Red Hills) and spans a 30×20 km area containing 29 land ownerships. Only 17% (n=35) of the cavity clusters within this core neighborhood occur on easements (which cover five properties). Two neighborhoods (Fig. 2) have become extinct since the first surveys of the region were conducted (Baker, 1995); neighborhood G became extinct in the early 1980s (Baker, 1983) and neighborhood C became extinct within the past 3 years. The fact that localized extinctions have occurred supports use of a metapopulation model (Gilpin, 1987), though neither neighborhood has been re-colonized.

Using stochastic simulations, the estimated chances of population persistence under the worst-case scenario of Status quo–Occupied Habitat (Table 3) were about 50:50. Improvements in habitat conditions within existing easements (Status quo–Potential Habitat) significantly improved the chances of persistence, to the point that more intensive management within existing easements could enhance population security more than random acquisition of 10,000–20,000 ha of new easements (Random 1 and 2) and almost as much as the random acquisition of 30,000 ha of new easements (Random 3).

Strategic scenarios generally provided much higher levels of security than Random scenarios (Table 3). With the exception of Strategic–Core Population (Sites A and B, Fig. 2), most probabilities of quasi-extinction for strategic scenarios were <10%. Given the fact that 95% confidence intervals for these probabilities were on the order of 0.03–0.05 (Table 3), only those scenarios at the extremes of the range of values had terminal quasi-extinction probabilities that were significantly different.

Comparisons of risk curves (Akcakaya and Root, 1998) and the Kolmogorov–Smirnov D-statistic (Table 4) suggested the scenario of Strategic–Small Populations was most similar to Total Protection in terms of the overall likelihood of persistence. However, this and several other Strategic scenarios with large new acreage totals probably will not be realized if the estimated ceiling of 20,000 ha of new easements is accurate. Only two scenarios had population survival probabilities.
4. Discussion

The approach taken for land conservation in the Red Hills will have a profound influence on the survival potential of this important population of red-cockaded woodpeckers. As measured simply by the number of active clusters conserved under different conservation scenarios, random selection of new conservation lands averaged 40–60% fewer active clusters than strategic selections of easements that focused more specifically on the spatial distribution of the population. Randomly acquired easements were significantly less likely to sustain the population even when the total area of conserved lands was more than doubled.

This was not a surprising result since only 31 of the 84 properties without easements have woodpeckers. However, the importance of focusing on key properties went beyond a simple focus on those properties with woodpeckers. Unless a regional approach is taken that considers the spatial configuration of woodpecker clusters, woodpecker clusters and habitat could become widely dispersed and the chances of long-term persistence lowered markedly.

Huxel and Hastings (1999) noted the need for regional planning in their theoretical analysis of patch occupancy in fragmented landscapes. An important spatial metric to be used in regional planning for red-cockaded woodpeckers is the number of active clusters within 2 km (Table 2). Hooper and Lennartz (1995) estimated that populations with <4.7 active clusters within 2 km had critically low densities, and the average number of active clusters within 2 km of inactive clusters in the Red Hills was 5.5 (Cox et al., unpub. data). The average densities of active neighbors produced under the Status quo, Random 1, and Random 2 scenarios were not significantly different than the 4.7 average cited by Hooper and Lennartz (1995) and were only half the current region-wide average for active clusters. A large proportion of the active clusters conserved under any random scenario thus would be prone to becoming inactive quickly.

A second measure of the importance of regional planning is found in results of the female-based model. If the Red Hills population of red-cockaded woodpeckers was restricted to existing conservation easements (Status quo–Occupied Habitat), we estimated from the model that the population would have about a 50% chance of persistence over 100 years (Table 3). Coupled with information on the dispersion of active clusters (Table 2) and results from the model developed by Letcher et al. (1998), the risk of population extinction under the worst-case scenario of Status quo–Occupied Habitat scenario is unacceptably high (Schafer, 1987). Our main focus centered on differences in survival potential as a function of changes in patterns of land conservation, but even under a scenario where management created suitable habitat throughout existing easements (Status quo–Potential Habitat), the population still appeared to face >10% chance of extinction without additional habitat conservation. In contrast, under the Total Protection scenario
scenario where all the near-cluster habitat was conserved, the population was estimated to have <1% of extinction over 100 years (Table 3), a level of risk that generally is deemed acceptably small. The 95% confidence intervals for these quasi-extinction probabilities ranged from 0.03-0.05 for all scenarios, so differences >10% were noteworthy.

Although strategic approaches provided better chances for long-term persistence, these scenarios could be constrained by another factor, namely the total area required to complete the different scenarios. The strategic scenarios that provided the best chances of long-term survival and required <20,000 ha (an estimated ceiling for new easements) were those that focused on properties within the core central neighborhood (Fig. 2, Area A). This neighborhood currently consists of 215 clusters, and six unprotected properties totaling 10,325 ha contain 52% of these clusters. As the Strategic–Large Populations scenario suggested, securing easements on four of these properties could improve the chances of population persistence to a level comparable to conservation of all remaining habitat (>90%).

Huxel and Hastings (1999) modeled population persistence in landscapes where habitat was lost and then restored in either a random or strategic manner. They found that populations responded well to randomly restored habitats if the total habitat covered >60% of the landscape. Below this threshold, strategically restored habitats were a better approach. The 60% threshold Huxel and Hastings (1999) described is similar to a threshold that we observed when we compared the number of active clusters conserved under the different random scenarios to the chances of long-term persistence. Once randomly selected properties conserved at least 60–70% of all the clusters, chances of long-term persistence were about the same as chances estimated for the Total Protection scenario where all clusters were conserved. Our samples were aggregated by property ownerships and thus were not truly random, but the value is within the general range observed by Huxel and Hastings (1999). This similarity may deserve further analysis and may relate to the phenomena conforming to a geometric distribution.

Fahrig (1997) used a spatially explicit model to tease apart the independent effects of habitat loss versus habitat fragmentation and concluded that habitat fragmentation was relatively unimportant. The dispersal routine used in Fahrig (1997) allowed for larger scale movements than red-cockaded woodpecker populations exhibit (Walters, 1990). In contrast, the model developed for red-cockaded woodpeckers by Letcher et al. (1998) showed that self-sustaining populations required nearly five-times as many territories in trials where territories were randomly dispersed versus trials where territories were clumped. The extent of the study area considered by Letcher et al. (1998) was nearly identical to the extent of the core neighborhood in the Red Hills (Fig. 2), and these results point to the potential importance of conserving aggregated habitat patches for species with low dispersal capabilities.

Practical conservation recommendations should be based on the scope of conservation measures likely to be undertaken in the near future as well as a consideration for the costs and benefits of different options (Montgomery, 1995). One cost/benefit consideration could be to minimize the acreage allocated for red-cockaded woodpecker conservation while maximizing the chances of long-term persistence. We estimate that populations of red-cockaded woodpeckers should have good chances of long-term persistence as long as the populations consist of ca. 120+ territories and these territories are spatially aggregated. Our recommendation for spatial aggregation would be to maintain an average of > seven active clusters within 2 km of each active cluster. These recommendations are based on results in Letcher et al. (1998) as well as the analyses presented here. For example, Letcher et al. (1998) found that proportionately fewer territories were occupied at the end of their simulations when the initial population size was <100 territories, and in our female-based model, the probability of quasi-extinction fell below 0.05 somewhere in the range of 120–180 territories.

Using these criteria, a very good spatial configuration of conservation easements for the core neighborhood would be the properties shown in Fig. 3. This hypothetical scenario involved 16,865 ha of new easement properties, and it conserved an additional 118 active clusters (total of 147 active and 61 inactive clusters). The mean number of active clusters within 2 km was 9.8, and populations on some of these properties could likely be increased with proper management. The model proposed by Letcher et al. (1998) suggested that populations of this general size were stable even when territories were widely dispersed, and our model suggested this population would have very high (>95%) chances of long-term persistence.

Turner et al. (1995) pointed out that models can also help conservation biologists explore the implications of planning efforts in situations where large-scale experiments are not feasible. The scenarios created under the subheading of Strategic–Expert Opinion (Table 1) provided a comparison of the potential outcomes of conservation planning based on general guidelines and expert opinion (Section 2) versus planning based on considerations for a rare species. Sites selected under the Strategic–Expert Opinion scenarios often excluded key properties in the core neighborhood and generally conserved smaller numbers of active clusters than other strategic scenarios. For example, the properties ranked highest by experts (Strategic–Highest Overall Score) did not include a property in the core neighborhood containing >18 active clusters. This property had a lower total...
score because of its lower wetland habitat and threat scores (Anon., 1996). Properties ranked for their connectivity similarly did not include an important parcel containing >24 clusters. Such omissions may reflect the complexity of integrating historical, biological, and recreational resources into a single conservation strategy (Schwartz, 1994), but the spatial distribution of red-cockaded woodpecker clusters needs to be given more consideration, especially since the various Strategic–Expert Opinion scenarios generally required large areas of new easements (c. 25,000 ha).

Persistence times estimated by metapopulation models are sensitive to the correlations established among population growth rates (Harrison and Quinn, 1989; LaHaye et al., 1994). This sensitivity exists in our model even though a high degree of correlation among neighborhoods was prescribed (>85%). It can be seen in the quasi-extinction probabilities estimated for the Strategic–Small Populations scenario, which mirrored the quasi-extinction probabilities estimated for Total Protection most closely (Table 3), as well as in comparisons of certain Random Easements. The Strategic–Small Populations scenario consisted of three neighborhoods >25 active clusters rather than a single larger neighborhood, and this scenario conserved woodpecker clusters throughout the current range in the Red Hills. This dispersion apparently enhanced population persistence slightly in comparison to other scenarios with less dispersion. In addition, when Random scenarios with at least two neighborhood populations >20 clusters were compared to Random scenarios having only a single population >40, the former group had average quasi-extinction probabilities that were about 20% lower than the latter group.

Letcher et al. (1998) did not include environmental stochasticity or environmental correlations in their model, but they suggested environmental correlations were probably important only if they were extreme. These results, coupled with other analyses (Harrison and Quinn, 1989; LaHaye et al., 1994), suggest environmental correlations need not be extreme to be influential. Interestingly, habitat quality, fire frequency and intensity, and other factors (Baker and Engstrom, 1995; Engstrom and Sanders, 1997) vary considerably among

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Fig. 3. Proposed arrangement of properties that will best conserve the central neighborhood of red-cockaded woodpeckers.
properties in the Red Hills, so environmental variation may be enhanced as much by the number of property ownerships in a given area as by the physical distances among groups of woodpeckers.

The slightly enhanced chances of persistence associated with greater geographic dispersion should not be used to argue for splitting up the core population. The difference in persistence times attributable to environmental correlations were very slight, and other evidence pointed to the importance of maintaining the core neighborhood in its current configuration. However, this result does suggest that attention should be given to some of the smaller, isolated neighborhoods in the Red Hills region (Fig. 3). Neighborhoods containing 25+ territories can persist for many decades (Walters, 1990; Letcher et al., 1998) and spread the risk of extinction (Gilmartin, 1987), and this becomes an especially prudent strategy to pursue if it is directed towards habitat improvement on existing easements. Most of the peripheral neighborhoods in the Red Hills currently are much smaller than 25 clusters, but construction of artificial cavities (Copeyon et al., 1991; Gaines et al., 1995; Watson et al., 1995) on properties with easements could be used to expand these populations quickly.

Current recovery goals developed for red-cockaded woodpeckers focus exclusively on federal lands (Lennartz and Henry, 1985) even though it seems unlikely the goals can be achieved in a reasonable time frame (James, 1995). The recovery goals for red-cockaded woodpeckers (and many other endangered species; Huxel and Hastings, 1999) also do not include consideration for the spatial arrangement of populations (Lennartz and Henry, 1985). Greater attention needs to be given to both issues, and expanded efforts to conserve this species on private lands in the Red Hills population should be based on a regional perspective. First and foremost, new conservation areas need to be secured within the core neighborhood, possibly through purchase of easements in key situations. Landowners in the core neighborhood also should be encouraged to participate in the “safe harbor” program (Costa, 1995) as a means of maintaining this neighborhood while habitat conditions and population numbers are improved elsewhere.

Attention also should be given to expanding populations and restoring habitat within existing easements. Properties likely will continue to be placed under easements in a random fashion as landowners seek tax advantages that easements provide, and a strong focus on management could help increase the geographic dispersion of populations significantly. As a first step, a more detailed evaluation of properties with conservation easements should be made to determine which easements are most likely to see short-term population increases. As Huxel and Hastings (1999) point out, this process can be improved through a consideration of the spatial arrangement of woodpecker clusters and potential management areas. Mitigation for the loss of habitat outside some of the critical areas described (e.g. Fig. 3) might be used to improve habitat conditions within easements and manage populations.

Finally, since the private lands considered here contain some of the best examples of mature longleaf pine habitat remaining in the southeastern USA (Engstrom and Baker, 1995), we consider these to be minimum recommendations that are relevant only if the total acreage conserved is in the range of 20,000 ha. Old-growth longleaf pine communities found in this region rank as one of the most imperiled communities of North America (Noss et al., 1999), and ideally we would hope to see a larger and more diverse assemblage of properties incorporated into a wide-spread group of conservation lands where red-cockaded woodpeckers, sports hunting, and timber management co-existed.

5. Uncited references

Brueckheimer, 1988; Dytham, 1995; Lamberson et al., 1992; Means, 1996; Saunders et al., 1991; Walters, 1991

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Appendix A. Demographic parameters used in the female-based population model.

Female life-history traits in red-cockaded woodpeckers more closely matched the parameters in RAMAS, so the stochastic population model was restricted to females. Some reasons for making this simplifying assumption were: territories of red-cockaded woodpeckers usually contain only one female (Walters, 1990); >99% of all females disperse from natal territories in their first year of life (Walters, 1990); females are capable of finding unmated males within fragmented habitats (Conner and Rudolph, 1991); young females disperse the greatest distance of any demographic cohort (Walters,
1990); and 10–35% of the clusters in a population may consist of solitary males (Walters 1990, James 1995), which suggests that the availability of females may limit populations in some instances. Males also represented a large proportion of the individuals counted in several declining populations (Baker, 1983; DeFazio et al., 1987; James. 1995; Reinman, 1995).

Stage structure

The female-based stage structure of the model was based on data presented in Stevens (1995) and produced a slightly expanding population ($\lambda = 1.0039$). The first stage consisted of birds of the year, which dispersed and produced fewer offspring than older groups. The second stage represented established breeders, which had higher survival than first-year birds but produced fewer offspring than older birds (Walters, 1990). The third stage represented females that had slightly lower productivity than females in the final stage (Lennartz et al., 1987). Based on an elasticity analysis (Caswell, 1989), the survival of first-year females, survival of adult females, and fecundity of first-year females were, respectively, the most important parameters affecting $\lambda$.

Dispersal

Red-cockaded woodpeckers generally disperse short distances to find a vacant territory (Walters, 1990), so dispersal of birds of the year was modeled as a density-dependent function. Females had lower chances of dispersing to other neighborhoods when carrying capacity in their natal neighborhood was low. The dispersal function used by RAMAS is:

$$M = e^{-D/b}$$

where $M$ is the proportion of females in the source population, $D$ is the distance between source and target populations, and $b$ is a constant representing the average distance a migrant travels. $b$ was set at 4.8 km (Walters, 1989), and $D$ was measured using the edge-to-edge distance among neighborhoods.

Carrying capacity

Carrying capacity is an important consideration in stochastic demographic models (Brook et al., 1997). Carrying capacity was established using a ceiling that was 15% larger than the size of the population that could be supported by near-cluster habitat. Since we use both active and inactive cavity clusters to define near-cluster habitat, we believe the ceiling reflected the habitat potential of the various properties. However, when initiating simulations, we used the number of active clusters as the starting population size.

Catastrophic events

Red-cockaded Woodpecker populations can be decimated by storms (Engstrom and Evans, 1990, Hooper et al., 1990), but catastrophic events were not modeled here.

Initial population abundances

 Initial abundances were set to approximate a stable-age distribution in each neighborhood. Abundances also were based on the number of active clusters present in each neighborhood.

Environmental and demographic stochasticity

Demographic and environmental stochasticity can be considered simultaneously in RAMAS Metapop (Açkayakaya and Root, 1998), so the option for demographic stochasticity was used. Procedures for establishing environmental stochasticity followed those outlined by Stevens (1995) where variation was set at 10% of the mean values. This was estimated as a “high” degree of variability in a study by Haig et al. (1993).

Environmental correlation

RAMAS Metapop creates correlation in environmental conditions among neighborhoods using the equation:

$$C_{ij} = a \exp( -D_{ij}^{c/b} )$$

where $a = 1.00$, $b = 1000.0$, and $c = 1.0$, and $D$ is the nearest edge-to-edge distance for neighborhoods measured in km. Even very widely dispersed neighborhoods had correlations > 85%.

Model evaluation

This model compared favorably with empirical data (Baker, 1983; Reinman, 1995) and an individually based model proposed by Letcher et al. (1998). For example, the 13 clusters originally found in neighborhood $G$ (Fig. 2) became extinct in < 10 years (Baker, 1983), and the female-based model predicted that 85% of the populations with similar initial sizes would become extinct within this time period. The model developed by
Letcher et al. (1998) did not include environmental stochasticity, but it suggested that small populations (ca. 25 territories) generally could persist for 100 years if territories were closely clumped. In this model, populations of 25 territories clumped in a single neighborhood had about a 50:50 chance of persisting 100 years.

References


