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Ecological Neighborhoods in Red-cockaded Woodpecker Populations

R. TODD ENGSTROM^{1,3} AND GRZEGORZ MIKUSINSKI²

¹Tall Timbers Research Station, Route 1, Box 678, Tallahassee, Florida 32312, USA; and

²Swedish University of Agricultural Sciences, Department of Conservation Biology, Grimso Wildlife Research Station, S-730 91 Riddarhyttan, Sweden

The spatial distribution of clusters of cavity trees has long been suspected to play an important role in population dynamics of the endangered Red-cockaded Woodpecker (*Picoides borealis*). Dependence on cavity trees probably played an essential role in the evolution of cooperative breeding behavior in Red-cockaded Woodpeckers (Walters 1990). Most young males adopt a strategy of either limited dispersal or helping, and young females (which are subordinate to all others in a group) almost always disperse (Walters et al. 1992). Woodpeckers that inhabit and defend a cluster of cavity trees—a single male, a pair, or a pair with one or more helpers—are called a “group.” Clusters are aggregations of living pine trees that have woodpecker cavities; they are termed “active” if currently in use and “inactive” and if currently unused.

Density is a common index of spatial distribution but is inadequate for populations that are distributed non-uniformly (Addicott et al. 1987). Defining the boundary of the area used to calculate density can be problematical, measuring suitable habitat to characterize the area included in density measurement is labor intensive, and the definition of suitable habitat may vary among populations. Whatever criteria are used to define an area, it is unlikely that an organism will be uniformly distributed within any but the most homogeneous landscape. Thus, a simple calculation of density disguises considerable variability in the distribution of individuals across a landscape. Consequently, a clear need exists to explore alternative methods to characterize the spatial distribution of Red-cockaded Woodpecker populations.

Many aspects of habitat affect the fitness of Red-cockaded Woodpeckers. Landscape features (e.g. fragmentation), cluster characteristics, and locations of clusters (e.g. isolation) also affect whether individual woodpecker cavity-tree clusters are active or inactive (Conner and Rudolph 1988, 1991, Thomlinson 1995). Conner and Rudolph (1988, 1991) used the number of active clusters within 2 km of a cluster as an index of isolation, but the number of active clus-

ters in an area also can be viewed as the “ecological neighborhood” that a dispersing individual is likely to encounter. Ecological neighborhoods are maintained mostly by short-distance dispersal that is typical of Red-cockaded Woodpeckers. In a population in North Carolina, the median dispersal distance of males and females is less than 5 km (Walters et al. 1988a), although dispersals of more than 90 km may occur (Walters et al. 1988b). Given the low frequency of long-distance dispersal (Walters 1991), it is not surprising that the ability of Red-cockaded Woodpeckers to locate and persist in cavity-tree clusters is negatively affected by cluster isolation and habitat fragmentation (Conner and Rudolph 1991, Thomlinson 1996).

We use the concept of an ecological neighborhood to compare five Red-cockaded Woodpecker populations. The ecological neighborhood, which is based on demography and dispersal, should not be confused with the genetic neighborhood (Wright 1943). A scale that reflects the importance of spatial arrangement of clusters and the social interactions among woodpecker groups can be based on dispersal distance. Therefore, we characterize ecological neighborhoods in two ways: (1) the number of neighbors (active woodpecker clusters) within the area of a circle with a radius of a typical dispersal distance, and (2) the distance from an active cluster to its tenth nearest neighbor. In this paper, we examine variation in ecological neighborhoods of five large populations of Red-cockaded Woodpeckers (143 to 494 groups each), discuss factors that contribute to this variation, and contrast our concept of ecological neighborhood with the traditional measure of density.

Study sites and methods.—We obtained data for Red-cockaded Woodpecker populations at Eglin Air Force Base (EAFB) in northwestern Florida, the Vernon Ranger District of the Kisatchie National Forest and Fort Polk (VRD-FP) in central western Louisiana, the Wakulla (WRD) and Apalachicola (ARD) Ranger Districts of the Apalachicola National Forest in the Florida panhandle, and the Red Hills (RH) hunting plantations between Tallahassee, Florida, and Thomsville, Georgia. The two ranger districts of Apalach-

³ E-mail: engstrom@bio.fsu.edu

icola National Forest are treated as separate populations because they are separated by the Ocklockonee River floodplain; the Vernon Ranger District and Fort Polk were combined because they are contiguous. Location of all known clusters was received either in digital format (Universal Transverse Mercator coordinates) or on maps. Cluster location and status (active or inactive) were collected during inventories from 1990 to 1994. Mapped clusters were digitized and entered into a geographic information system (GIS; Environmental Systems Research Institute, Inc. 1992) for analysis.

We used the median dispersal distance of males in a North Carolina population (4.5 km; Walters et al. 1988a) as the radius of a circle that defines a neighborhood. The number of neighbors was the number of active clusters within a 4.5-km radius around a cluster. To assess the sensitivity of our use of 4.5 km to define a neighborhood, we also calculated neighborhoods using a 3.2-km distance. The center of the circle either was the centroid of globally located (Global Positioning System) cavity trees within a cluster (ARD, WRD, FP), a visual estimate of the centroid of a cluster (EAFB, VRD), or approximate cluster location on a topographic map (RH). We measured the number of neighbors for all active and inactive clusters for all five populations and summarized the distribution of the number of neighbors in histograms.

In addition to the number of neighbors, we were interested in the distance that an individual must travel to explore its neighborhood. This distance reflects the effort that must be made to search for openings (death of a breeder) within neighboring groups. In any year, only a few breeders will die within an ecological neighborhood. We calculated the first, fifth, and tenth nearest-neighbor distances for each active cluster in each population to provide a distance measure of the neighborhood.

Differences between active and inactive clusters were compared with Mann-Whitney tests. Pearson correlation coefficients were derived to compare similarity of the number of neighbors within 4.5 km and the distances to the first, fifth, and tenth nearest neighbors.

Traditional calculation of density is the number of individuals (or groups in this case) per unit area of suitable habitat. Suitable habitat in the four populations on public land was easy to calculate because forest management treatments are relatively consistent within stands. For our purposes, we defined suitable habitat on public lands (ARD, EAFB, VRD-FP, and WRD) as any pine-dominated forest that was at least 30 years old. The amount of habitat that is suitable for Red-cockaded Woodpeckers within the Red Hills, however, is problematical, because management activities are not as consistent or clearly defined. For comparative purposes, we used the approximate area of the 28 plantations that have active

TABLE 1. Number of clusters and median neighborhood size for active and inactive clusters within each of five Red-cockaded Woodpecker populations.

Cluster status	n	No. of neighbors		
		Median	$\bar{x} \pm SD$	Range
Red Hills				
Active	178	29	29.7 \pm 14.0	0 to 57
Inactive	66	13	16.3 \pm 15.8	0 to 58
Vernon Ranger District-Fort Polk				
Active	221	28	27.0 \pm 11.0	4 to 51
Inactive	95	24	23.2 \pm 13.7	0 to 52
Apalachicola Ranger District				
Active	494	26	25.7 \pm 9.2	0 to 46
Inactive	109	29	27.3 \pm 10.3	4 to 46
Eglin Air Force Base				
Active	214	18	17.9 \pm 9.1	1 to 36
Inactive	266	9	10.9 \pm 9.6	0 to 36
Wakulla Ranger District				
Active	143	8	8.0 \pm 3.6	1 to 17
Inactive	144	8	8.1 \pm 3.7	2 to 18

Red-cockaded Woodpecker clusters as an estimate of the amount of suitable habitat. A more accurate measurement of the area of suitable habitat within the Red Hills is beyond the scope of this study.

Results.—The median number of neighbors for the five populations ranged from 29 active clusters within 4.5 km of an active cluster at RH to 8 active clusters at WRD (Table 1). The maximum number of neighbors ranged from 17 at WRD to 57 at RH. The proportion of the population that had a small number of neighbors (0 to 9 active clusters) ranged from 14% at WRD to <1% at VRD-FP (Fig. 1). The ranked order of the populations was the same whether the radius that defined the neighborhood was 4.5 km or 3.2 km.

The number of neighbors around inactive clusters was significantly smaller than the number around active clusters at RH, VRD-FP, and EAFB (Mann-Whitney test, $P < 0.05$) but not at ARD and WRD (Table 1, Fig. 1). The first, fifth, and tenth nearest-neighbor distances also were significantly different (Mann-Whitney test, $P < 0.05$) between active and inactive clusters in the RH, VRD-FP, and EAFB populations (with the exception of VRD-FP first nearest-neighbor distances; $P > 0.10$). Nearest-neighbor distances between active and inactive clusters on ARD and WRD were not significantly different.

We compared population density (total number of active clusters/amount of suitable habitat) with the density of active clusters within the 4.5-km radius neighborhood (Table 2). Average population density within suitable habitat corresponded closely with density within the 4.5-km radius neighborhood for

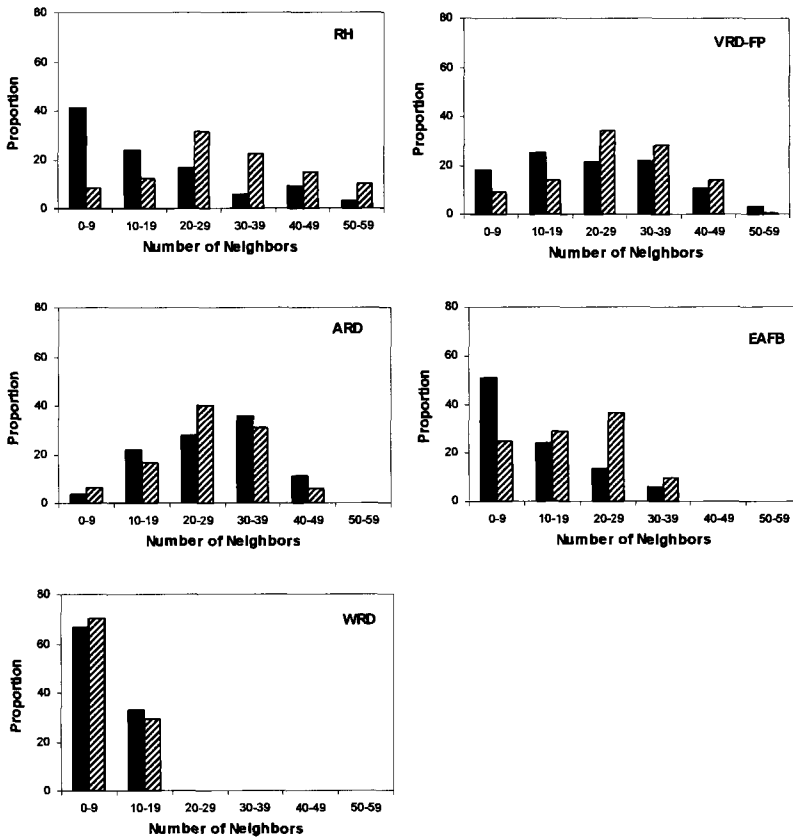


FIG. 1. Distributions of the number of neighbors of inactive (solid black) and active clusters (diagonal lines) in five Red-cockaded Woodpecker populations based on the number of active clusters within 4.5 km of each cluster. RH = Red Hills; VRD-FP = Vernon Ranger District-Fort Polk; ARD = Apalachicola Ranger District; EAFB = Eglin Air Force Base; WRD = Wakulla Ranger District.

all populations except ARD and WRD (Table 2). At ARD and WRD, density based on the amount of suitable habitat was more than three times greater than density within the 4.5-km radius neighborhood.

Median distances to the first, fifth, and tenth nearest neighbors were similar for all populations except WRD, where distances were approximately twice the

distances in the other populations (Fig. 2). All of the correlation coefficients between the number of neighbors and first, fifth, and tenth nearest-neighbor distances were significant (after Bonferroni adjustment for multiple testing). As expected, the correlation coefficient between the number of neighbors within 4.5 km and the first nearest-neighbor dis-

TABLE 2. Two calculations of density for five populations of Red-cockaded Woodpeckers.

Population	Total area (km ²)	Suitable habitat (km ²)	Density	
			Suitable habitat ^a	Median no. neighbors ^b
Apalachicola Ranger District	1,161	341	1.45	0.41
Vernon Ranger District-Fort Polk	703	444	0.50	0.40
Red Hills	1,520	423	0.42	0.46
Wakulla Ranger District	1,082	345	0.41	0.13
Eglin Air Force Base	1,876	789	0.27	0.28

^a Number of active clusters per km² of suitable habitat.

^b Median number of neighbors divided by area of a 4.5-km circle (63.59 km²).

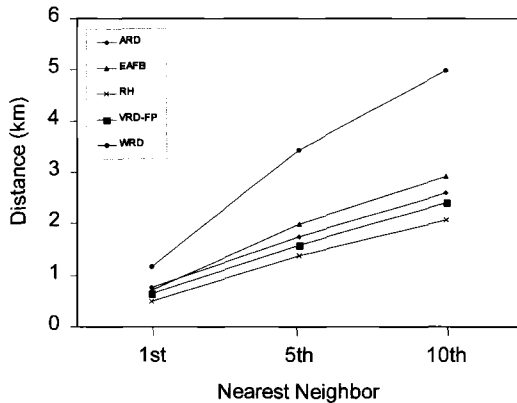


FIG. 2. Median distance to first, fifth, and tenth nearest neighbors from active clusters in the five study populations of Red-cockaded Woodpecker. ARD = Apalachicola Ranger District; EAFB = Eglin Air Force Base; RH = Red Hills; VRD-FP = Vernon Ranger District-Fort Polk; WRD = Wakulla Ranger District.

tances ($r = -0.477$, $P < 0.01$) was considerably lower than that between the number of neighbors and tenth nearest-neighbor distances ($r = -0.780$, $P < 0.01$).

Discussion.—Density within an ecological neighborhood may play an important role in the likelihood of successful colonization of unoccupied habitat (Gilpin and Hanski 1991, Verboom et al. 1991) and the cost of dispersal forays (Matthysen et al. 1995a,b). Red-cockaded Woodpecker clusters persist via occupation by a group, or by being captured by a nearby group (Doerr et al. 1989). As in the Eurasian Nuthatch (*Sitta europaea*; Matthysen 1990), young Red-cockaded Woodpeckers frequently probe into neighboring territories (R. T. Engstrom pers. obs.). In dense neighborhoods, any opening created by the death of a breeder would be filled quickly by the high number of potential colonists from the surrounding groups. In contrast, isolated clusters have a higher incidence of abandonment (Conner and Rudolph 1991; Thomlinson 1995, 1996).

The estimation of density—the number of individuals divided by area—is complicated by the problem of defining the relevant area. Interstices of unoccupied space within a sample area are an automatic by-product of imposing boundaries (Campbell 1995). Red-cockaded Woodpecker foraging habitat can be quantified, but its value depends on the availability of cavity trees (Copeyon et al. 1991). The number of neighbors, easily calculated by using GIS, provides a functional measure of local density for each group that is based on the median dispersal distance of a well-studied population in North Carolina (Walters et al. 1988a).

To some degree, any measures of density and def-

initions of ecological neighborhoods are arbitrary and population-specific. Although dispersal distances vary among populations, we feel that defining a local reproductive neighborhood based on dispersal distances of a real population is explicit and reasonable (Addicott et al. 1987). Likewise, nearest-neighbor distances are significantly correlated with the number of neighbors in our study populations. Use of the number of neighbors calculated for each cavity-tree cluster, or of the distance needed to travel to a given number of neighbors, provide reasonable means of scaling that permit comparisons of the same species among different environments.

We found that density of Red-cockaded Woodpecker neighborhoods varied widely within and between populations. Within populations, some active clusters were completely isolated and some were surrounded by up to 57 groups. Among the five study populations, the median number of neighbors was 3.6 times larger at RH than at WRD. Likewise, the median distance to the tenth nearest neighbor for active clusters in the WRD was twice that for the other populations (Fig. 2). The significance of the relatively low number of neighbors at WRD is unclear, but the population is declining (James et al. 1997). James et al. (1997) speculated that woodpeckers in WRD suffer from a nutrient deficiency mediated by a change in fire history. The median number of neighbors among the other populations (RH, ARD, VRD-FP, EAFB) is similar. Forests in RH, the population that has a marginally larger number of neighbors, have been managed by single-tree or small-group selection methods within an uneven-aged silvicultural approach (Engstrom and Baker 1995, Engstrom et al. 1996). Existing and potential replacement cavity trees on many of the hunting plantations were protected intentionally. Considering the high number of neighbors at RH, forest management practices used there deserve attention.

In three of the five populations (RH, EAFB and VRD-FP), inactive clusters had significantly smaller neighborhood sizes than active clusters (Table 1, Fig. 1). Thomlinson (1995) also determined that inactive clusters were more isolated than active clusters in Texas. Neighborhood sizes of active clusters at ARD and WRD, however, were the same or slightly smaller than those in inactive clusters (Table 1). Cavities in these inactive clusters may be of such low quality that they are not used even when many woodpecker groups occur in the area.

We offer several hypotheses to test the effects of neighborhood density on Red-cockaded Woodpecker dispersal and cluster persistence. First, persistence of cluster activity should be longer in denser populations, because an opening caused by the death of a breeder is more likely to be filled than in a more dispersed neighborhood. Second, denser neighborhoods should have more helpers (but see Conner and Rudolph 1991) and should be more productive over

a long period. Of course, the quality of habitat is influenced by more than the number of neighbors. The quality and number of cavities within a cluster and foraging-habitat quality also are very important. Evaluation of the components of habitat quality could be approached experimentally by using artificial cavities (Copeyon et al. 1991) to manipulate cluster density, foraging-habitat quality, and number of cavity trees per cluster. Such an approach would be useful to evaluate the relative importance of selected extrinsic influences on delayed dispersal and the probability of persistence of populations of Red-cockaded Woodpeckers.

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What is the Function of First Eggs in Crested Penguins?

COLLEEN CASSADY ST. CLAIR¹

Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019, USA

Crested penguins (genus *Eudyptes*) have attracted considerable attention for the small size of their first-laid eggs. Depending on the species, the first egg is 15 to 45% smaller than the second (Warham 1975), the largest dimorphism known in birds (Slagsvold et al. 1984). Disadvantages accrued by smaller size are accentuated by reversed hatching asynchrony (first eggs hatch after second eggs), thereby defining an atypical system of brood reduction in which first eggs seldom survive to produce a fledgling. In other brood-reducing nonpasserines, egg size decreases with laying order, and first-laid eggs are more likely to survive (see Slagsvold et al. 1984, Williams 1994). These differences have prompted two unanswered questions concerning crested penguins (Johnson et al. 1987, Lamey 1990): why are first eggs smaller, and why are two eggs produced?

Questions about the function of first eggs are encouraged by the exceptional patterns of egg loss in three of the six species of *Eudyptes*. In Macaroni Penguins (*E. chrysolophus*; Gwynn 1953, Williams 1980, Williams 1989), Royal Penguins (*E. schlegeli*; Carrick 1972, St. Clair et al. 1995), and Erect-crested Penguins (*E. sclateri*; Richdale 1941, Miskelly and Carey pers. comm.), first eggs typically disappear from nests soon after laying. Most of these losses occur immediately before second eggs are laid (Williams 1989, St. Clair et al. 1995), and deliberate ejection by

female parents is the overwhelming cause of this mortality in Royal Penguins (St. Clair et al. 1995). Such early losses preclude most of the insurance or replacement function of first-laid eggs (sensu Mock and Parker 1986, Forbes 1991, Mock and Forbes 1995), and the timing of losses suggests that whatever function first eggs have is limited to the four-day laying interval between first and second eggs. Functions during this time may include limited insurance against occasional failure to lay a second egg (Williams 1989, St. Clair and St. Clair 1996), or secondarily derived functions that do not require the continued survival of first eggs. Because crested penguin eggs likely are inexpensive to produce (Williams 1990), and much selective inertia would attend the evolution of a single-egg clutch (St. Clair et al. 1995), even weak secondary functions during the laying interval may confer measurable benefits.

Several secondary functions have been suggested, although none has yet been tested. For example, first eggs may: (1) provide a signal to conspecifics that the nest site is occupied (Johnson et al. 1987), thus reducing contests over nesting space prior to the laying of the second egg; (2) enhance laying synchrony (Johnson et al. 1987) by providing a visual stimulus that quickens laying by surrounding pairs; (3) enhance mate attraction for young or first-time breeders by providing a visual indication of a female's preparedness to reproduce; and (4) provide an important tactile stimulation for formation of the brood patch (i.e. incubation patch), thereby enhancing the thermal environment of second eggs (St. Clair 1992). This secondary function could operate in both sexes but might be particularly important in males be-

¹ Present address: Biology Programme, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia V2N 4Z9, Canada
E-mail: stclairc@unbc.ca