

Reoccupation of Abandoned Clusters of Cavity Trees (Colonies) by Red-cockaded Woodpeckers

Phillip D. Doerr, *Departments of Zoology and Forestry, North Carolina State University, Campus Box 7617, Raleigh, NC 27695*

Jeffrey R. Walters, *Department of Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695*

J. H. Carter III, *Department of Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695*

Abstract: We documented red-cockaded woodpecker (*Picoides borealis*) occupation of cavity tree clusters on North Carolina study areas from 1980–88. Most occupied cavity tree clusters (93%) were used in consecutive years, but 6.8% were abandoned each year. Abandoned sites were captured or reoccupied at an annual rate of 8.7%, implying there is a 60% chance that an abandoned site will be reoccupied in a 10-year period. However, recently abandoned clusters were reoccupied at a much higher rate than long-abandoned clusters. Cluster occupation was dynamic with some being occupied, abandoned and reoccupied, or captured during our study. Cluster use by solitary males often was intermediate temporally between group occupation and abandonment. Habitat enhancement may improve reoccupation rates and could be an important short-term strategy to increase the number of social units of this endangered species. Cavity tree clusters are an important resource that should be conserved, irrespective of current activity status.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 43:326–336

The endangered red-cockaded woodpecker is endemic to mature pine forests in the southern United States (DeLotelle and Epting 1988) where the woodpeckers excavate cavities in living pines. Groups of 2–7 birds, or occasionally an unpaired male, occupy a cluster of cavity trees. Cavity trees average 70–95 years old at initiation of cavity construction, and 150 years is typical of many trees (Lennartz et al. 1983, Wood 1983). Suitable habitat typically consists of frequently burned, mature stands with an open understory. The endangered status of the red-cockaded woodpecker is associated with a dramatic decline in the availability of mature second

growth and old growth longleaf pine (*Pinus palustris*) in the southern United States (Wahlenberg 1946, Lennartz et al. 1983, Ligon et al. 1986). Red-cockaded woodpeckers also inhabit mature loblolly (*P. taeda*), slash (*P. elliotii*), pond (*P. serotina*), and shortleaf pines (*p. echinata*), but seem to prefer longleaf.

The formation of new clusters of cavity trees by red-cockaded woodpeckers in previously unoccupied habitat (colonization) occurs rarely (Hooper 1983, Walters et al. 1988). Therefore, land managers are faced with the dual challenges of protecting existing populations from further decline and promoting expansion. Red-cockaded woodpeckers may expand an area of occupied habitat very slowly by excavating cavities in suitable trees somewhat distant from clusters already in use (pioneering) (Hooper 1983). By this process, new clusters of cavity trees may be formed. New groups also form by territorial budding in which 1 territory and its cavity trees are split into 2 clusters (Hooper 1983, Walters 1989).

The slow rate of population expansion emphasizes the importance of maintaining existing habitat in suitable condition. One factor that threatens existing populations is the deterioration of occupied habitat: hardwoods invading pure pine stands during succession. This process is usually arrested in natural forests by the frequent occurrence of summer wildfires. Some authors have suggested (Beckett 1971) that red-cockadeds abandon cavity tree clusters where hardwood understory reaches the height of cavity openings. This response is often cited as the reason that unoccupied (abandoned) clusters of cavity trees occur. On our North Carolina study areas (Carter et al. 1983, Walters et al. 1988), 30% of the 414 sites we monitored from 1981 through 1988 were abandoned at any given time.

We present evidence that abandoned clusters are important to maintaining extant populations of red-cockaded woodpeckers. These clusters may provide the best short-term opportunity to enhance the habitat available to the birds and thus increase the number of groups in populations.

Our research was funded by the National Science Foundation (BSR-8307090 and BSR-8717683), the U.S. Fish and Wildlife Service via Section 6 of the Endangered Species Act of 1973 administered through the North Carolina Wildlife Resources Commission, the North Carolina Agricultural Research Service at North Carolina State University, Department of the Army, Fort Bragg, and donations from various individuals and conservation organizations. We thank private landowners for access to their lands, and the commanding general, Fort Bragg Military Reservation, for access to that facility. Personnel of the Fish and Wildlife Branch, Fort Bragg, under the direction of M. Hunnicutt assisted. We also appreciate the cooperation of personnel from the North Carolina Wildlife Resources Commission during our work on the Sandhills Game Lands. R. Blue, C. Copeyon, J. Hammond, J. Harrison, M. LaBranche, J. Lape, P. Manor, R. Repasky, M. Reed, P. Robinson, T. Stamps and several undergraduate interns assisted in data collection. J. DeFrazio, R. Lancia, M. Lennartz, and R. Powell provided helpful comments on previous drafts of the manuscript. The North Carolina Agricultural Research Service provided administrative and logistic support.

Study Areas

Our study areas were located in the Sandhills of south-central North Carolina. The habitat was largely second-growth longleaf pine with scattered old-growth trees, a scrub oak (*Quercus spp.*) midstory and wiregrass (*Aristida stricta*) ground cover. While open savannah occurs widely, fire exclusion has permitted dense hardwood midstory and understory encroachment in some areas. Dendritic drainages with poorly drained soils supported pocosin vegetation characterized by an overstory of pond pine. Loblolly pine occurred on wetter soils and frequently was mixed with longleaf pine on old field sites.

The study areas encompassed >130,000 ha and supported about half of central North Carolina's red-cockaded woodpeckers. The region was subdivided into 4 study areas: SOPI includes the resort and residential towns of Southern Pines and Pinehurst and numerous horse farms, SGL encompassed the federally owned land managed by the North Carolina Wildlife Resources Commission, FB comprised the western one-third of Fort Bragg military reservation, and MIN was an area of mixed agricultural land and woodlands located between the other areas. Detailed descriptions of these areas are available in Walters et al. (1988).

Methods

The results reported in this paper are based on annual breeding censuses and monitoring of reproductive activities at all known cavity tree clusters on our study areas since 1981. Our preference for cavity tree "cluster" over "colony" is detailed by Walters et al. (1988). Virtually all adult and nestling red-cockaded woodpeckers on our areas have been marked with unique combinations of color bands.

Designation of clusters is critical to our analysis. We wished to retain information about the changing use of trees, and so used the criteria detailed by Walters et al. (1988). These criteria define clusters based on use by birds and spatial arrangement of trees.

Each spring from 1980–88 we visited all clusters in our study areas to determine whether they were active or abandoned, using Jackson's (1977) activity criteria. Clusters with at least 1 active cavity tree were considered occupied and those lacking active cavities were considered abandoned. Abandoned clusters were visited only once during a given breeding season, unless the cluster had been occupied the previous breeding season. In that event, we resurveyed the area to attempt to locate undetected cavity trees. Failure to locate new cavity trees terminated our breeding season effort at that cluster. Recently abandoned clusters were revisited in late summer or fall to check for activity. We defined "cluster-year" to designate a cluster observed for consecutive breeding seasons. All methods used in our long-term studies of red-cockaded woodpeckers in North Carolina are presented in detail by Walters et al. (1988). Chi-square analyses were used to test the distribution of cluster transition frequencies for independence among study areas.

Results

Within each year from 1980 through 1988, the proportion of active clusters averaged 70%, and ranged from 64%–83%. Active clusters were occupied by groups, occupied by solitary males, or captured (that is, used by groups residing in other, nearby clusters). Across all study areas and years, 53.7% of 2,767 cluster-years involved clusters that were occupied by groups of woodpeckers at the beginning of the cluster-year. Overall, we observed that only 0.9% of clusters occupied by groups at the beginning of the cluster-year were abandoned at the end, but that 2.6% were captured and 5.1% were occupied by solitary males (Fig. 1). Captured clusters usually were taken over by groups of birds that continued to use their original cluster.

The rate of formation of new clusters, which occurred exclusively by territorial budding, was extremely low (Fig. 1): only 6 cases were observed, which represented an annual probability per cluster of only 0.4%.

Generally, abandoned clusters remained unoccupied. Of 837 cluster-years in which the cluster was abandoned at the beginning of the cluster-year, 764 (91.3%) remained unoccupied. In other words, 8.7% of abandoned clusters were reoccupied each year. If probability of reoccupation were constant across clusters and across years, the probability of a cluster persisting as abandoned for consecutive cluster-years is 0.834 or $(0.915)^2$, and the probability of remaining abandoned for 10 consecutive years is only 0.402. That is, there is a 60% chance that an abandoned cluster will be reoccupied within a 10 year period. However, clusters did not appear to be reoccupied with equal likelihood. Of the 88 clusters that were abandoned at

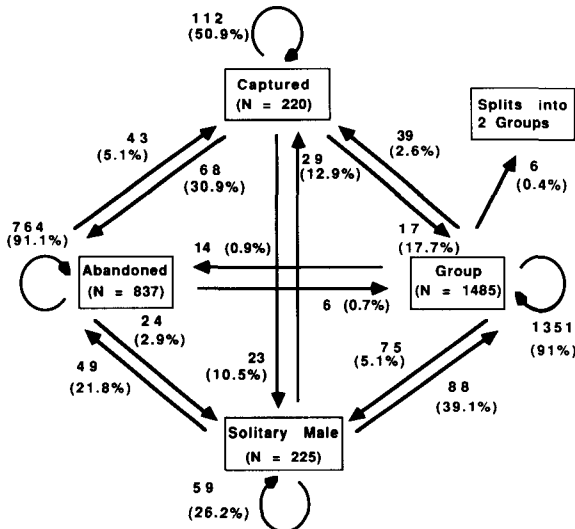


Figure 1. Annual transition frequencies and probabilities (in parentheses) for red-cockaded woodpecker cavity tree clusters on 4 North Carolina study areas, 1981–88; *N* is number of cluster-years in sample.

the beginning of the study, only 14 (15.9%) were reoccupied during the study. In contrast, 43 of 91 (52.7%) clusters abandoned during the study were reoccupied. Thus, recently abandoned clusters were more likely to be reoccupied than long-abandoned clusters. Only 4 (4.5%) clusters abandoned at the beginning of the study were occupied by groups, compared to 17 (18.7%) abandoned during the study.

Clusters abandoned in 1 year were much more likely to be captured (43) cases or occupied by a solitary male (24 cases) in the subsequent year than to be occupied by a group (6 cases). Similarly, clusters that initially a group occupied were more likely to be captured (39 cases) or occupied by a solitary male (75 cases) than to be completely abandoned the next year (14 cases). Thus, being captured and being used by a solitary male were transitional stages between being occupied by a group and being abandoned (Fig. 1).

Captured clusters are active clusters, but do not represent breeding groups. Being captured preceded abandonment (Fig. 1), but clusters had a high probability of being wrested from their captors by new groups in subsequent years. Of 220 cluster-years in which the cluster was captured at the beginning of the year, 7.7% were occupied by new, independent groups at the end of the year. More often, captured clusters remained captured, were abandoned, or were occupied by a solitary male. Of 98 clusters captured at some time during the study, 30 (30.6%) subsequently housed breeding groups.

Clusters housing a solitary male were even more likely to subsequently house a breeding group. Of 135 clusters housing a solitary male at some time during the study, a group later occurred in 86 (63.7%). The annual probability of transition from a solitary male to a group was 39.1%. However, the solitary male stage was followed by total abandonment nearly as often (Fig. 1).

Chi-square analysis revealed that the probabilities of transition between occupancy states were not equal among study areas. Clusters were least likely to continue to house groups in MIN and SOPI, and most likely to in FB (Table 1). FB, which had the smallest proportion of abandoned clusters, consistently exhibited the largest mean group size within a given year (Table 2). Abandoned clusters were most likely to remain abandoned in MIN and SOPI, and least likely to remain abandoned in FB (Table 3). In addition, abandoned clusters were most likely to be captured in FB and least likely to be captured in SOPI and MIN (Table 3). Also, clusters were less likely to remain captured in SOPI than in the other study areas, although this difference was not significant (Table 4). Clusters housing solitary males were most likely to continue to house solitary males and least likely to change to housing a group in SOPI (Table 5).

Overall, then, transitions were most likely to lead toward abandonment and away from occupancy by a group in MIN and SOPI, and least likely to lead toward abandonment in FB. These same trends were evident in following clusters over several transitions, as well as in annual probabilities of transitions. In this analysis, MIN was divided into 2 portions, 1 including several small concentrations of clusters (MIN 1) and the other including the remaining clusters, which were scattered widely over a large area (MIN 2). Of 33 clusters abandoned at the beginning of the study

Table 1. Transition frequencies of cavity tree clusters occupied by groups of red-cockaded woodpeckers at beginning of cluster-year on 4 North Carolina study areas 1981–88.^a

Study area	Group continues to use		Becomes abandoned		Solitary male uses		Another group captures		Total N cluster-years ^b
	N	%	N	%	N	%	N	%	
SOPI	331	90.2	3	0.8	23	6.3	10	2.7	367
SGL	386	91.3	2	0.5	22	5.2	13	3.1	423
FB	506	93.9	3	0.6	17	3.2	13	2.4	539
MIN	134	85.9	6	3.8 ^c	13	8.3	3	1.9	156
Total	1,357	91.4	14	0.9	75	5.1	39	2.6	1,485

^aSum Chi-Square (test of independence, 9 df) = 23.61, $P < 0.005$.

^bCluster-year is a cavity tree cluster followed for 2 consecutive breeding seasons.

^cDenotes cells contributing most to chi-square sum.

in MIN 2, only 1 (3.0%) was reoccupied subsequently. In contrast, 3 of 7 in FB were reoccupied (42.9%), and in SOPI, SGL, and MIN 1, 19 of 48 were reoccupied (18.8%). Of those abandoned during the study, 4 of 18 in FB (22.2%); 31 of 62 in SGL, SOPI, and MIN 1 (50.0%); and 8 of 11 in MIN 2 (72.7%) remained abandoned. Of those clusters that housed solitary males, only 27 of 55 in SOPI and MIN 2 subsequently were used by groups (49.1%), whereas 59 of 80 in FB, SGL, and MIN 1 were (73.8%).

Discussion

Our data suggest that occupation, abandonment, and reoccupation of clusters of cavity trees is a dynamic process, although rates of change are clearly low. Instances in which a cluster is suddenly abandoned are few, as are instances in which an abandoned cluster is occupied by a new social group. There is usually a transition stage of being captured or being occupied by a solitary male between being abandoned and being occupied by an independent group.

Table 2. Mean size of red-cockaded woodpecker groups and overall percentage of clusters abandoned on 4 North Carolina study areas, 1981–87.^a

Study area	1981	1982	1983	1984	1985	1986	1987	Clusters abandoned (%)
FB	2.31	2.32	2.34	2.30	2.60	2.51	2.39	11.6
SGL	2.15	2.03	2.09	2.07	2.27	2.25	2.28	26.4
SOPI	2.06	2.17	2.00	2.18	2.38	2.22	2.21	37.8
MIN	1.88	1.93	2.11	2.15	2.32	2.25	2.30	52.0

^aFB group size significantly larger each year ($F = 89.2, P < 0.0001$).

Table 3. Transition frequencies of cavity tree clusters abandoned at beginning of cluster-year on 4 North Carolina study areas, 1981–88.^a

Study area	Remain abandoned		Captured		New group occupies		Solitary male occupies		Total <i>N</i> cluster-years ^b
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	
SOPI	280	93.0	9	3.0	2	0.7	10	3.3	301
SGL	186	89.4	13	6.2	2	1.0	7	3.4	208
FB	68	78.2	16	18.4 ^c	0	0.0	3	3.4	87
MIN	230	95.4	5	2.1	2	0.8	4	1.7	241
Total	764	91.3	43	5.1	6	0.7	24	2.1	837

^aSum Chi-square (test of independence, 9 df) = 38.81, $P < 0.005$.

^bCluster-year is a single cluster followed for 2 consecutive breeding seasons.

^cDenotes cell contributing most to chi-square sum.

In a typical sequence, an abandoned cluster is activated by an existing group (captured). A male then wrests the captured cluster from this group to form a new social unit, which at first is a solitary male unit. This male eventually attracts a mate to form a new breeding unit.

Abandonment usually begins with the loss of a breeding female from a group. The remaining male fails to attract a mate, and the social unit enters the solitary male phase. When the male dies, the cluster is captured by a neighboring group. Eventually the group ceases to use the captured cluster, and it becomes abandoned.

Although these sequences are typical, they are by no means inevitable. Some clusters have shifted back and forth between being abandoned and captured, without ever being occupied by a new social unit. Others have shifted between being captured and being occupied by a solitary male. Sometimes being occupied by a solitary male represents a brief interlude during which a male is unpaired in a cluster that houses

Table 4. Transition frequencies of cavity tree clusters captured at beginning of cluster-year on 4 North Carolina study areas, 1981–88.^a

Study area	Become abandoned		Remain captured		Solitary male occupies		New Group occupies		Total <i>N</i> cluster-years ^b
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	
SOPI	15	35.7	13	31.0	7	16.7	7	16.7	42
SGL	27	31.0	49	56.3	6	6.9	5	5.7	87
FB	20	26.3	43	56.6	8	10.5	5	6.6	76
MIN	6	40.0	7	46.7	2	13.3	0	0.0	15
Total	68	30.9	112	50.9	23	10.5	17	7.7	220

^aChi-square (test of independence, 9 df) = 14.44; $P > 0.10$.

^bCluster-year is a cavity tree cluster followed for 2 consecutive breeding seasons.

Table 5. Annual transition frequencies for cavity tree clusters occupied by solitary male red-cockaded woodpeckers at the beginning of a cluster year on 4 North Carolina study areas 1981–88.^a

Study area	Remain solitary		Captured		Group occupies		Becomes abandoned		Total <i>N</i> cluster-years ^b
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	
SOPI	33	39.3 ^c	10	11.9	21	25.0	20	23.8	84
SGL	10	17.9	8	14.3	26	46.4	12	21.4	56
FB	7	15.2	9	19.6	25	54.3	5	10.9	46
MIN	9	23.1	2	5.1	16	41.0	12	30.8	39
Total	59	26.2	29	12.9	88	39.1	49	21.8	225

^aSum chi-square (test of independence, 9 df) = 26.119, $P < 0.005$.

^bCluster-year is a cluster followed for 2 consecutive breeding seasons.

^cDenotes cells contributing most to chi-square sum.

a group in all other years, rather than a transitional stage. Some clusters remain captured for long periods without ever being abandoned or occupied by a new group.

Captured clusters sometimes become the focus of activity of the groups that capture them. Captured clusters initially are used as a roost site for 1 or more group members. Often it is the female, who has the lowest priority in intra-group competition, who roosts in the captured cluster. However, groups shifted their nest site to the captured cluster 39 times. The original cluster is then used primarily for roosting, and may even be abandoned. In some instances new groups have occupied the original cluster after the group moved to the captured cluster. Thus it is possible for groups to shift their location through this process. It is also possible for a previously abandoned cluster to be used for breeding through this process. Abandoned clusters thus may be useful to existing groups, as well as to newly formed groups.

Some authors suggest that habitat deterioration is a principal cause of abandonment of cavity tree clusters by red-cockaded woodpeckers (Beckett 1971, Van Balen and Doerr 1978). Hardwood understory and mid-story growth is thought to block cavity entrances and interfere with flight paths through the cavity tree cluster (Van Balen and Doerr 1978, Jackson 1978, Repasky 1984). Habitat deterioration via hardwood encroachment is but 1 plausible explanation for cluster abandonment. Lack of cavities, regardless of understory, is another (see below). Poor habitat conditions, resulting from factors other than understory, may contribute to the probability that all members of the group might either disperse, or die. This combination of events is probably rare when habitat quality is high since adult red-cockaded woodpeckers exhibit annual survival rates of over 70%, and only 13% of adult survivors are likely to disperse (Walters et al. 1988).

It is inevitable that habitat quality differs among clusters of cavity trees. Thus, some abandoned clusters are more likely to be reoccupied than others. Our data fit this scenario. Some clusters appear to be marginally acceptable, adequate to attract

dispersing birds, but not of high enough quality to hold them long. The small fraction of abandoned clusters that subsequently housed groups supports this notion. Most abandoned clusters have not attracted any birds during our study, suggesting serious habitat deterioration occurred there. Recently abandoned sites are most often reused, and these likely contain better habitat than those long abandoned. The number and quality of cavities and associated foraging areas are likely important features of the habitat affecting occupation, as is the presence or absence of cavity competitors. Our current experiments with artificially constructed cavities indicate that the lack of suitable cavities may be a factor in reoccupation of some clusters. Such clusters, like those suffering from understory encroachment, can be rehabilitated and thus have high potential for reoccupancy. Those abandoned because of a loss of foraging base, in contrast, have little chance of reoccupancy over the short run. Factors other than those that originally caused abandonment may affect reoccupancy, since habitat may change over time. Deterioration of cavities may be especially important in this regard.

We emphasize the reoccupation rates reported here occurred largely in the absence of management. We predict that silvicultural treatment will increase the rate of reoccupation of abandoned clusters and decrease abandonment rates, though this must be tested. Differences between study areas may support this notion. The only study area in which abandoned clusters were rehabilitated, primarily through understory clearing, was in FB, and abandoned clusters were reoccupied at a significantly higher rate here than in all other study areas. However, FB also has the densest woodpecker population, which may contribute to the high level of use of habitat. Clusters whose occupants perish are more likely to be located by new birds if the surrounding population is substantial. The area with the lowest density of birds, MIN 2, exhibited the lowest rates of reoccupancy and highest rates of abandonment. Not only does this area have a sparse population, but it is also at the periphery of the Sandhills population. It appears that the processes by which deceased individuals are replaced operate less effectively at the periphery of the population. It may also be that habitat is poorest at the periphery. SOPI has a fairly high density of birds, but much of it is also peripheral in location. This may be a factor in the low rate of return of clusters with solitary males to group status. SGL, FB and MIN 1 are located in the interior of the greater Sandhills population. It seems apparent that dispersal is a significant factor in continued occupancy of sites, and that a peripheral location reduces chances of dispersal into a cluster.

Management Implications

Our observations have several implications for management. First, highest priority must be given to protecting existing woodpecker sites. An occupied cluster has a higher probability of being used in the future than a vacant site. Clearly, captured clusters and those occupied by solitary males have a high likelihood of being returned to group status. There is potential to attract red-cockaded woodpeckers

to abandoned sites, especially if the reasons for abandonment can be reversed by management. This is, in our view, a compelling argument to retain abandoned clusters, given that the average age of cavity trees invariably exceeds 60–95 years (DeLotelle and Epting 1988, Hooper 1988) and many decades are required to grow new habitat. Abandoned clusters of cavity trees should be conserved and managed for conditions that exist on areas inhabited by red-cockaded woodpeckers.

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