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RED-COCKADED WOODPECKER RECOVERY: AN INTEGRATED STRATEGY

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Abstract: Populations of the red-cockaded woodpecker (Picoides borealis) have experienced massive declines since European colonization of North America. This is due to extensive habitat loss and alteration. Logging of old-growth pine forests and alteration of the fire regime throughout the historic range of the species were the primary causes of population decline. Listing of the red-cockaded woodpecker under the Endangered Species Act of 1973, as amended, and increased emphasis on management of non-game species have resulted in efforts to recover remnant populations of the red-cockaded woodpecker in many parts of its historic range. Due to extensive research and adaptive management initiatives much is now known about the elements required for both short- and long-term management of viable populations of red-cockaded woodpeckers. A short-term strategy is crucial because currently available habitat, in nearly all populations, is poor in 1 or more critical respects. Consequently, almost all populations require immediate attention in the short term, to insure suitable midstory and understory conditions, adequate availability of suitable cavities, and restoration of demographic viability through improvements in number and distribution of breeding groups. Management techniques including artificial cavities, cavity entrance restrictors, translocation of birds, prescribed fire, and mechanical and chemical control of woody vegetation are available to achieve these needs. In the long term, cost-effective management of red-cockaded woodpecker populations requires a timber management program and prescribed fire regime that will produce and maintain the stand structure characteristic of high quality nesting and foraging habitat, so that additional intensive management specific to the woodpeckers is no longer necessary. Timber management that achieves this goal and still allows substantial timber harvest is feasible. The implementation of a red-cockaded woodpecker management strategy, as outlined above, represents appropriate ecosystem management in the fire-maintained pine ecosystems of the southeastern United States and will ultimately benefit a great number of additional species of plants and animals adapted to this ecosystem.

Key words: management, *Picoides borealis*, population dynamics, prescribed fire, recovery strategy, red-cockaded woodpecker.

The total population of red-cockaded woodpeckers at the time of European colonization of North America has been estimated to have ranged from 920,000 (Costa 2001) to in excess of 1.5 million groups (Conner et al. 2001a). By the last quarter of the 20th century, Jackson (1978a) estimated the rangewide population at <4,000 groups and approximately 10,000 individuals. More recent estimates placed the population at 4,029 (James 1995) to 4,694 (Costa and Walker 1995) active clusters. This massive decline precipitated the designation of the red-cockaded woodpecker as an endangered species in 1970 by the U. S. Bureau of Sport Fisheries and Wildlife. It was also listed as endangered when the ESA was first enacted in 1973. Extensive research since Ligon's (1970) seminal paper, to which the 4 red-cockaded woodpecker symposia to date bear witness, have provided researchers, managers, and policy makers with the ecological knowledge and management tools to effect the recovery of red-cockaded woodpeckers on a portion of their former range.

The comprehensive recovery strategy for the red-cockaded woodpecker we advocate was first described as "the new management strategy" in Conner et al. (2001a). The necessity of ongoing, enlightened management is abundantly clear. Not only do populations perform poorly where management is poorly designed, but even in situations where forest management is minimal, i.e. wilderness areas, populations continue to decline (Wood and Lewis 1977, Saenz et al. 2001b). In this paper we describe the management strategy we advocate and its basis in knowledge of population dynamics.

CAUSES OF POPULATION DECLINE

The massive population decline of the red-cockaded woodpecker is a result of numerous alterations of the forest landscape interacting with the unique biology of the species. These interactions explain why most coexisting avian species have not suffered similar declines and provide the basis for the recovery strategy described in Conner et al. (2001a) and in this paper (see also U. S. Fish and Wildlife Service 2003).

It is often instructive to think about populations in terms of carrying capacities and vital rates. In the case of red-cockaded woodpeckers, we can define the carrying capacity as the number of potential territories available, which is a function of the quantity and quality of appropriate habitat. Vital rates, in this context, are birth and survival rates characteristic of a population. Various measures, for example clutch size, number of fledglings, and population turnover rates, provide information on vital rates.

Carrying Capacity

Viewed in this context, the decline of the red-cockaded woodpecker has resulted primarily from changes in carrying capacity. It has been estimated that 100 million ha of pine habitat were present in what is now the southeastern United States when Columbus landed in 1492 (Conner et al. 2001a). In 2000 the land base remaining in some type of forest was estimated at 60 million ha, 60% of the original figure (Conner et al. 2001a). The harvest of the old-growth pine forests of the southeastern United States, culminating in eastern Texas and the Ouachita Mountains of Arkansas during the first third of the 20th century, accounts for a substantial portion of the observed decline in carrying capacity and consequently in red-cockaded woodpecker populations.

The quality of the remaining pine habitat also impacts carrying capacity. Pine forests existing today are generally characterized by younger tree age, lower rates of red heart (*Phellinus pini*) infection, increased abundance of woody vegetation in the midstory and understory, and greater habitat fragmentation. Logging of the original forests followed by short-rotation timber harvest with increasing emphasis on pulp and wood chip products, rather than sawtimber, have greatly altered the age structure of pines throughout the region (Wahlenberg 1946, 1960, Frost 1993). Alteration of fire regimes, generally to less frequent fire return intervals and less effective fires, has also been widespread (Frost 1993). The profound effects of changes in fire regimes on all aspects of fire-maintained pine communities are only beginning to be appreciated (Platt et al. 1988b, Bridges and Orzell 1989, Weigl et al. 1989, Christensen 1993, Frost 1993, James et al. 1997, Rudolph and Burgdorf 1997).

These factors impact carrying capacity in 2 principal ways: negative effects of the encroachment of woody vegetation and reduced availability of suitable cavities. Suitable cavities for roosting and nesting are a critical resource that may have driven the evolution of cooperative breeding in red-cockaded woodpeckers (Copeyon et al. 1991, Walters et al. 1992a, Conner and Rudolph 1995a, Ligon 1999). The unusual population dynamics are such that red-cockaded woodpeckers will typically only occupy territories with existing cavities (Copeyon et al. 1991, Walters et al. 1992a, Conner et al. 2001a); however, see Walters (2004). The excavation of cavities exclusively in living pines places substantial constraints on excavation dynamics. Consequently, average excavation times range from 2-13 years, depending on pine species and location (Conner and Rudolph 1995a, Harding and Walters 2004). Multiple causes of cavity loss also exist and can be substantial (Conner et al. 1991, Conner and Rudolph 1995b, Harding and Walters 2002). The availability of suitable cavities, dependent on the relationship between rates of cavity excavation and loss, is an important determinant of carrying capacity.

In recent decades nearly all forests supporting red-cockaded woodpeckers have been characterized by a low availability of potential high quality cavity trees (Ligon 1970, Jackson et al. 1979, Conner and Rudolph 1989, Costa and Escano 1989, Rudolph and Conner 1991). The suitability of potential cavity trees increases with development of adequate heartwood diameters at increasing heights, and incidence of red heart decay that facilitates excavation (Conner et al. 1994). Since tree diameter and age are partially correlated, the suitability of potential cavity trees increases with age. The harvest of older pines and intensive silvicultural practices that essentially eliminate older trees, which are the potential cavity trees, effectively reduces the carrying capacity to zero.

Altered fire regimes impact carrying capacity by promoting the development of hardwood midstory. Encroachment of woody vegetation in the vicinity of potential cavity trees reduces their suitability, and also leads to abandonment of existing cavities (Conner and Rudolph 1989, 1991a; Loeb et al. 1992). The negative effect of encroachment of woody vegetation has been a common theme in the decline of red-cockaded woodpecker populations (Wood 1983a; Hovis and Labisky 1985; Conner and Rudolph 1989, 1991a; Costa and Escano 1989; Davenport et al. 2000).

Loss of existing cavities is another contributing factor in reduced carrying capacity. Younger trees typically have cavities at lower average heights, which may result in increased ignition of the resin barrier and destruction of the cavity during fires (Conner et al. 1991). Changes in pine species due to silvicultural practices or alteration of the fire regime often result in replacement of longleaf pine (*Pinus palustris*) with species, most frequently loblolly pine (*P. taeda*), that are more susceptible to southern pine beetle (*Dendroctonus frontalis*) mortality, ultimately increasing the rate of cavity tree loss (Frost 1993, Conner and Rudolph 1995b). In some areas, enlargement of cavities by other species of primary cavity excavators, primarily pileated woodpeckers (*Dryocopus pileatus*), can be the leading cause of loss of existing cavities (Conner et al. 1991, Harding 1997, Saenz et al. 1998b, Harding and Walters 2002). These factors, combined with reduced availability of potential cavity trees, may exceed the ability of red-cockaded woodpeckers to maintain sufficient numbers of suitable cavities through time.

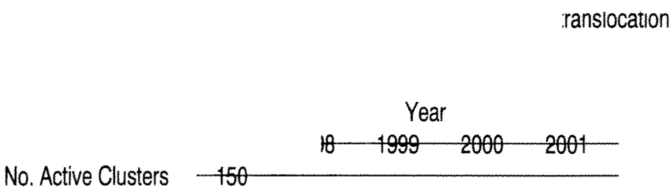
The quality of foraging habitat is also reduced by encroachment of woody vegetation and reduced tree age. Recent studies have shown that red-cockaded woodpeckers tend to avoid foraging in dense midstory vegetation (Rudolph et al. 2002, Walters et al. 2002b). Other studies have raised the possibility that habitat quality declines when the herbaceous understory of grasses and forbs is reduced due to encroachment of woody vegetation (James et al. 1997, 2001), perhaps because of lower prey abundance (Collins et al. 2002, Taylor and Walters 2004). Red-cockaded woodpeckers also show a preference for larger and older trees for foraging (Skorupa 1979, Engstrom and Sanders 1997, Zwicker and Walters 1999, Walters et al. 2002b). Groups are larger and more productive when their foraging stands are more similar in structure to historic pine stands, that is, when they contain an open canopy of large pines, little midstory, and abundant and diverse groundcover (James et al. 1997, 2002; Walters et al. 2002b). When foraging habitat deviates from this condition, each woodpecker group likely requires more of it, further reducing carrying capacity.

As the carrying capacity of the landscape declines due to alterations of the foraging habitat and limitations on cavity availability, red-cockaded woodpecker populations become increasingly reduced in size and isolated. Habitat fragmentation due to land use patterns also exacerbates isolation (Conner and Rudolph 1991b, Rudolph and Conner 1994). Currently, most populations are small and extremely isolated from other typically small populations (Jackson 1978a, James 1995, Conner et al. 2001a). This situation, ultimately due to declines in carrying capacity, results in the potential for genetic and demographic problems (Conner and Rudolph 1989, Stangel et al. 1992, Haig et al. 1993, Daniels and Walters 2000a). Demographic and genetic factors have the potential to drive continuing population declines, even if the original habitat alterations that reduced carrying capacity are mitigated.

Vital Rates

A surprising result of demographic studies of red-cockaded woodpeckers is that population trends are insensitive to changes in rates of reproduction and mortality (Lennartz and Heckel 1987, Walters et al. 1988a, Walters 1990a, LaBranche and Walters 1994). In existing populations, reproduction and survival rates reported from declining populations tend to be similar to those from stable and increasing populations. This result is due, in part, to the buffering effect of helpers (Conner et al. 2001a, Walters et al. 2002a). Increases in reproduction or mortality in any given year do not result in more occupied territories, but rather in increases or decreases in the size of the helper and floater classes. It is rare for suitable territories to be unoccupied because there are too few individuals to fill them. Typically, populations, even declining ones, remain at or near carrying capacity as determined by the presence of suitable territories with adequate cavities. Populations decline because territories are lost, although vital rates in the remainder of the population remain unchanged.

An instructive example (Table 1) is provided by the recent history of the red-cockaded woodpecker population on the Sam Houston National Forest in Texas. Between 1997 and 2001 this population of 150-168 active groups, with an estimated annual production of 229-284 fledglings per year, was a donor population for a major translocation program on the West Gulf Coastal Plain. During this period an average of 33.2 subadult red-cockaded woodpeckers was removed from the population per year, a total representing 13.3% of the estimated reproductive output. During this same period the population increased from 150 to 168 active clusters. Thus, a large and sustained decrease in a vital rate (i.e., fledgling production) did not preclude population increase. This suggests a lack of dependence of population change on vital rates. It also demonstrates that populations can be heavily harvested to support translocation efforts without leading to population declines.



Summary of Population Decline

In summary, red-cockaded woodpeckers were presumably once distributed in large, continuous populations throughout a large range. Following European colonization, habitat alterations reduced carrying capacity and populations declined dramatically. The primary causes were harvesting of old-growth pine forest and alteration of the fire regime in remaining pine habitat. In contrast, red-cockaded woodpecker populations, due to their social system, are well buffered from population declines due to changes in vital rates. Given suitable habitat, vital rates remain adequate in most existing populations in most years.

INTEGRATED RECOVERY STRATEGY

The recovery strategy for red-cockaded woodpecker populations presented here is based on the premise that population declines have resulted primarily from declines in carrying capacity rather than change or variation in vital rates. Consequently, management must address those factors that have reduced carrying capacity in the past and still continue to do so in the present. Conversely, management that attempts to improve vital rates, such as southern flying squirrel (*Glaucomys volans*) control, will have minimal impact on the number of groups in a population. Such activities are generally not cost effective, except in very small red-cockaded woodpecker populations where stochastic losses of single birds are significant.

Due to the critical status of most existing red-cockaded woodpecker populations, short-term strategies are generally required. Long-term strategies are also required to control economic costs and avoid issues associated with single-species management. The long-term strategies presented here are also compatible with, and conducive to, appropriate ecosystem management required to achieve the natural biodiversity of fire-maintained pine communities in the southeastern United States.

The management strategy we advocate (Conner et al. 2001a) is an integrated approach that addresses the requirements of red-cockaded woodpecker recovery while maintaining overall ecosystem function. Based on the outline above, 3 potential causes of population decline must be assessed. If any 1 of the 3 exists, management action will be required to prevent further population decline and ultimately achieve recovery.

Midstory Condition

Midstory vegetation, especially hardwood midstory, must be maintained at, or reduced to, acceptable levels. If encroachment is extensive, rapid control may not be possible with prescribed fire alone, and mechanical or chemical means may be required (Costa and Escano 1989). Transition to a long-term strategy based on prescribed fire and a compatible silvicultural system should be the ultimate goal. Maintaining an acceptable level of woody vegetation in the midstory and understory reduces the probability of territory abandonment, potentially increases the available prey base, and increases productivity.

Cavity Availability

The availability of suitable cavities must be assured. Implementation of a management protocol that insures adequate cavities will reduce territory abandonment. Two complementary approaches address the availability of cavities in the short term. Cavity restrictors can be used to rehabilitate cavities where the entrance tube has been partially enlarged or to prevent enlargement from occurring (Carter et al. 1989). The development of techniques to construct artificial cavities, either drilled cavities (Copeyon 1990) or cavity inserts (Allen 1991), provides managers with almost complete control over cavity availability. In the long term, a silvicultural system must be adopted that will provide adequate numbers of high quality, potential cavity trees well dispersed across the landscape. This will allow cavity excavation rates by the woodpeckers to balance cavity losses, thus maintaining an adequate number of suitable cavities to prevent population declines due to insufficient cavities. Multiple options are available depending on pine species, potential fire regimes, and other management needs (Rudolph and Conner 1996, Engstrom et al. 1996, Hedrick et al. 1998).

Demographics and Fragmentation

The related issues of population demographics and habitat fragmentation must be addressed if they are preventing population recovery. The goal is a population of sufficient size and spatial distribution such that demographic viability is achieved without intensive management. Habitat restoration can reduce habitat fragmentation in both the short term and long term, and should be considered where feasible. Very often, however, habitat restoration requires too much time to be sufficient. In the short term 2 very powerful techniques are available to rapidly improve population demographics. The creation of new cavity tree clusters (recruitment clusters) with suitably reduced midstory and adequate artificial cavities is straightforward. These should be placed such that they improve the spatial configuration of the overall population (Conner and Rudolph 1991b, Copeyon et al. 1991). New clusters should be placed in sites that create aggregations of territories within the relatively short dispersal distances of helpers (Walters et al. 1988a, 2002a). The development of translocation techniques allows managers to establish potential breeding groups in clusters containing solitary birds (DeFazio et al. 1987, Hess and Costa 1995), and to introduce pairs to vacant habitat (Rudolph et al. 1992) with a high degree of success (Carrie et al. 1999). It is now feasible to effectively counter the effects of habitat fragmentation and small population size in the short term. In the long term, management that provides large blocks of habitat with adequate carrying capacity and relatively large populations will preclude negative impacts due to genetic and demographic factors.

ADDITIONAL MANAGEMENT OPTIONS

Additional management options, 2 in particular, are frequently discussed in relation to red-cockaded woodpecker management. Each attempts to effect an improvement in vital rates, by reducing predation or cavity competition, thereby increasing fledging rates and (hopefully) leading to population growth. As we have argued above, modest changes in vital rates will not have an appreciable impact on population growth. In a species with very high fledging rates, such as the red-cockaded woodpecker, very modest increase in fledgling numbers is all that is possible.

Control of Snake Predation

Due to their well-developed climbing abilities, rat snakes (*Elaphe* spp.) are efficient predators of avian eggs and nestlings. The evolution of resin well excavation by red-cockaded woodpeckers was presumably driven by selection pressure due to snake predation (Ligon 1970; Dennis 1971b; Jackson 1974, 1978b; Rudolph et al. 1990b), as the resin barrier provides substantial protection from predation by rat snakes (Jackson 1974, 1978b; Rudolph et al. 1990b). Although there is a remarkably high rate of climbing attempts by rat snakes on red-cockaded woodpecker cavity trees (Neal et al. 1993a), there are no data to suggest that rat snakes can overcome resin barriers with sufficient frequency to have more than a minor effect on reproductive rates.

The development of techniques using netting, metal excluders, and bark shaving has provided the means to reduce snake predation on red-cockaded woodpeckers in cavities (Withgott et al. 1995, Saenz et al. 1998a). If not lethal to the snakes, i.e. netting, these methods are appropriate to reduce mortality in extremely small red-cockaded woodpecker populations. They are also appropriate in situations where the resin barrier is compromised, e.g., newly installed artificial cavities occupied before the resin barrier is well established. General use of these methods in an attempt to increase reproductive rate and promote population growth is ill advised, and will not be cost effective. The potential increase in fledging success is minimal and any increase will not alter population size.

Control of Flying Squirrels

Southern flying squirrels are frequent inhabitants of red-cockaded woodpecker cavities (Dennis 1971a, Harlow and Lennartz 1983, Rudolph et al. 1990a, Loeb 1993, Conner et al. 1996, Kappes 1997). It has been suggested that flying squirrels detrimentally impact red-cockaded woodpeckers due to cavity kleptoparasitism or predation on eggs or nestlings. Four studies address these issues. Two (Rudolph et al. 1990a, Mitchell et al. 1999) detected no significant reduction in reproductive output of red-cockaded woodpeckers due to flying squirrels. The other 2 (Loeb and Hooper 1997, Laves and Loeb 1999) did detect impacts attributable to flying squirrels, but in both cases the effect, although statistically significant, was fairly small.

Because population changes are insensitive to moderate changes in vital rates, management to reduce flying squirrel impacts is generally ineffective. Management using metal excluders to prevent access to cavities (Montague et al. 1995) or removal of squirrels (Franzreb 1997a) may be beneficial (Brown and Simpkins 2004, Hagan et al. 2004, Poirier et al. 2004, Stober and Jack 2004) (and is hopefully cost effective) only in very small red-cockaded woodpecker populations where individual birds are critical.

Conflicts with Other Priorities

Efforts to reduce the impacts of rat snakes and flying squirrels may conflict with other conservation priorities. Except in very small red-cockaded woodpecker populations, an effective program to control snakes or flying squirrels is both expensive and labor intensive. Money and labor may be diverted from management directed at increasing carrying capacity (prescribed burning, cavity management, translocation) that is critical for population growth. Obviously diverting resources to management activities that produce minimal population benefits at the expense of management activities that produce substantial population gains is poor management practice.

Other than removal of exotics, single-species management activities that directly target other species, rat snakes and flying squirrels in this instance, are generally unwise. The goal of red-cockaded woodpecker management should be to return this species to its natural role in the ecosystem, which includes providing cavities for southern flying squirrels and prey for rat snakes. Fortunately, the impacts of southern flying squirrels and rat snakes are on vital rates, rather than on carrying capacity, and are not a critical determinant of population behavior.

A species that does impact carrying capacity, the pileated woodpecker, does require management, namely protection of cavities from enlargement by use of metal restrictors (Saenz et al. 1998b). This presumably has minimal impact on pileated woodpecker populations. Even in this case, large red-cockaded woodpecker populations in forests with abundant potential cavity trees of high quality will likely suffer less detrimental impact from pileated woodpeckers than currently occurs.

MANAGEMENT EXAMPLES

The management strategy we advocate has been adopted as the management philosophy at numerous locations, several of which are highlighted in Table 2. Not all aspects of the strategy have been adopted in all cases, and on occasion additional techniques (i.e. to improve vital rates) have been used. However, we believe that sufficient management attention has been directed at carrying capacity issues in these cases, to result in population increases with or without the additional efforts to improve vital rates. One of these cases (Camp Lejeune) is discussed in further detail elsewhere (Walters 2004).

The philosophy embodied in the new management strategy allowed managers to effectively mitigate the impacts of Hurricane Hugo on the red-cockaded woodpecker population of the Francis Marion National Forest (Watson et al. 1995). This major hurricane in September 1989 reduced the population on the forest from approximately 470 groups to 249 groups, many with only a single bird by the 1990 breeding season. Recognition that lack of suitable cavities was the

Table 2. Results of implementation of the new management strategy in selected red-cockaded woodpecker populations.

Population	Years	Habitat Management	Cavity Availability	Demographics	Population Response
Camp Lejeune	1986-91	Modest fire	No management	No management	Stable at 27-31
	1991-98	Huge fire effort	Cavity management	No management	Increase from 27 to 46
Croatan Natl. Forest	Pre-1990	Minimal fire	No management	No management	Declining to 38
	1990-95	Huge fire effort	Cavity management	Translocation	Increase from 38 to 57
Savannah River	Pre-1985	Minimal fire	No management	No management	Declined to 1
	1985-95	Substantial fire	Cavity management	Translocation	Increased to 20
Natl. Forests in Texas	Pre-1990	Minimal fire	No management	No management	Declining 8-10% per yr
	1990-01	Modest fire	Cavity management	Translocation	Increase from 223 to 281

primary factor limiting carrying capacity, and the then recent development of artificial cavity technology, drove the rapid response to the critical needs of this population. Installation of hundreds of artificial cavities increased the number of groups with 2 or more birds to 353 by 1994.

Interruptions in the implementation of the new management strategy due to conflicting priorities and legal actions also provide insight. At Camp Lejeune a moratorium on the installation of new recruitment clusters resulted in a reduction in the rate of population growth in the late 1990s. Subsequent creation of additional recruitment clusters has resulted in a return to rapid population growth (Walters 2004).

In Texas, lawsuits filed by environmental groups have, ironically, impeded implementation of critical management of red-cockaded woodpeckers. In recent years these suits have restricted the ability of managers of the national forests to conduct prescribed burns and other management activities necessary to restore and maintain suitable vegetation structure in forests degraded by a long history of fire suppression and an inadequate prescribed burning regime. As a result, red-cockaded woodpecker population increase has been erratic in recent years (Rudolph et al. 2004a).

SUMMARY

The management strategy we advocate is based on the premise that changes in carrying capacity drive the population dynamics of red-cockaded woodpeckers. Consequently, effective management must address the critical determinants of carrying capacity, i.e., fire-maintained pine forests of appropriate age and structure, adequate cavity availability, and population size and distribution of woodpecker groups. Red-cockaded woodpecker population change, expressed as number of groups, is remarkably insensitive to changes in vital rates. Management that attempts to improve vital rates is generally not necessary, and diverts resources from the critical management of carrying capacity. Experience has demonstrated that where carrying capacity issues have been adequately addressed, populations remain stable or increase. Where 1 or more of these issues has not been adequately addressed, populations decline. We feel that it is already evident that other management strategies are not as effective, or as cost effective, as the one we advocate.

Sufficient knowledge and technology is currently available to implement short-term and long-term management to recover red-cockaded woodpecker populations. The ultimate outcome of red-cockaded woodpecker management and recovery depends, not on the knowledge and technology necessary to accomplish recovery, but on the trade-offs with other management objectives. The new recovery plan for the species (U. S. Fish and Wildlife Service 2003) emphasizes the elements of the management strategy we advocate. We urge managers to select from the options available to them in the recovery plan in order to implement the management strategy we describe.

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LITERATURE CITED

Allen, D. H. 1991. An insert technique for constructing artificial red-cockaded woodpecker cavities. Gen. Tech. Rep. SE-73. 19pp

Bridges, E. L., and S. L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Nat. Areas J. 9:246-263.

Brown, C., and S. Simpkins. 2003. The Chickasawhay Ranger District story: saving a small population from extirpation *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, WA. In press.

Carrie, D. 2003. Effects of removing subadult birds to translocation on an east Texas red-cockaded woodpecker donor population *in* R. Costa and S.J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, WA. In press.

Carrie, N. R., R. N. Conner, D. C. Rudolph, and D. K. Carrie. 1999. Reintroduction and postrelease movements of red-cockaded woodpecker groups in eastern Texas. J. Wild. Manage. 27:824-832.

Carter, J. H., III, J. R. Walters, S. H. Everhart, and P. D. Doerr. 1989. Restrictors for red-cockaded woodpecker cavities. Wildl. Soc. Bull. 17:68-72.

Christensen, N. L. 1993. The effects of fire on nutrient cycles in longleaf pine ecosystems. Proc. Tall Timbers Fire Ecol. Conf. 18:205-225.

Collins, C. S., R. N. Conner, and D. Saenz . 2002. Influence of hardwood midstory and pine species on pine bole arthropods. For. Ecol. Manage. 164: 211-220.

Conner, R. N., and D. C. Rudolph. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett and Sabine National Forests. Res. Paper SO-250. 15pp

Conner, R. N., and D. C. Rudolph. 1991a. Effects of midstory reduction and thinning in red-cockaded woodpecker cavity tree clusters. Wildl. Soc. Bull. 19:63-66.

Conner, R. N., and D. C. Rudolph. 1991b. Forest habitat loss, fragmentation, and Red-cockaded Woodpecker populations. Wilson Bull. 103:446-457.

Conner, R. N., and D. C. Rudolph. 1995a. Excavation dynamics and use patterns of red-cockaded woodpecker cavities: Relationships with cooperative breeding. Pages 343-352 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies, College of Forestry, Stephen F. Austin State University. Nacogdoches, Texas.

Conner, R. N., and D. C. Rudolph. 1995b. Losses of red-cockaded woodpecker cavity trees to

southern pine beetles. Wilson Bull. 107:81-92.
Conner, R. N., D. C. Rudolph, D. L. Kulhavy and A. E. Snow. 1991. Causes of mortality of red-cockaded woodpecker cavity trees. J. Wildl. Manage. 55:531-537.
Conner, R. N., D. C. Rudolph, D. Saenz, and R. R. Schaefer. 1994. Heartwood, sapwood, and fungal decay associated with red-cockaded woodpecker cavity trees. J. Wildl. Manage. 58:728-734.
Conner, R. N., D. C. Rudolph, D. Saenz, and R. R. Schaefer. 1996. Red-cockaded woodpecker nesting success, forest structure, and southern flying squirrels in Texas. Wilson Bull. 108:697-711.
Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The red-cockaded woodpecker: surviving in a fire-maintained ecosystem. Univ. Texas Press, Austin, Tx. 363 pp.
Copeyon, C. K. 1990. A technique for constructing cavities for the red-cockaded woodpecker. Wildl. Soc. Bull. 18:303-311.
Copeyon, C. K., J. R. Walters, and J. H. Carter. 1991. Induction of red-cockaded woodpecker group formation by artificial cavity construction. J. Wildl. Manage. 55:549-556.
Costa, R. 2001. Red-cockaded woodpecker. Pages 309-321 *in* J. G. Dickson, ed. Wildlife of southern forest: habitat and management. Hancock House Publishers, Blaine, Wa.
Costa, R., and R. E. F. Escano. 1989. Red-cockaded woodpecker: status and management in the southern region in 1986. Tech. Pub. R8-TP 12. 71pp
Costa, R. and J. L Walker. 1995. Red-cockaded woodpecker. 1995. Pages 86-89 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, and others, eds. Our living resources: a report to the nation on the distribution, abundance, and health of U. S. plants, animals, and ecosystems. U. S. Natl. Biol. Serv., Washington, D. C.
Daniels, S. J., and J. R. Walters. 2000. Inbreeding depression and its effects on natal dispersal in Red-cockaded Woodpeckers. Condor 102:482-491.
Davenport, D. E., R. A. Lancia, J. R. Walters, and P. D. Doerr. 2000. Red-cockaded woodpeckers: a relationship between reproductive fitness and habitat in the North Carolina Sandhills. Wildl. Soc. Bull. 28:426-434.
DeFazio, J. T., M. A. Hunnicutt, M. R. Lennartz, G. L. Chapman, and J. A. Jackson. 1987. Red-cockaded woodpecker translocation experiments in South Carolina. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 41:311-317.
Dennis, J. V. 1971. Species using red-cockaded woodpecker holes in northeastern South Carolina. Bird-banding 42:79-87.
Engstrom, R. T., and E. J. Sanders. 1997. Red-cockaded woodpecker foraging ecology in an old-growth longleaf pine forest. Wilson Bull. 109:203-217.
Engstrom, R. T., L. A. Brennan, W. L. Neel, R. M. Farrar, S. T. Lindeman, W. K. Moser, and S. M. Herman. 1996. Silvicultural

practices and red-cockaded woodpecker management: a reply to Rudolph and Conner. Wildl. Soc. Bull. 24:334-338.
Franzreb, K. E. 1997. Success of intensive management of a critically imperiled population of red-cockaded woodpeckers in South Carolina. J. Field Ornithol. 68:458-470.
Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Tall Timbers Fire Ecol. Conf. 18:17-44.
Hagan, G., R. Costa, and M. K. Phillips. 2003. The first reintroduction of red-cockaded woodpeckers into unoccupied habitat: a private land and conservation success story *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, WA. In press.
Haig, S. M., J. R. Belthoff, and D. H. Allen. 1993. Population viability analysis for a small population of red-cockaded woodpeckers and an evaluation of enhancement strategies. Conserv. Biol. 7:289-301.
Harding, S. R. 1997. The dynamics of cavity excavation and use by the red-cockaded woodpecker (*Picoides borealis*). M.S. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Vi.
Harding, S. R., and J. R. Walters. Processes regulating the population dynamics of red-cockaded woodpecker cavities. J. Wildl. Manage. 66:1083-1095.
Harding, S. R., and J. R. Walters. 2003. Dynamics of cavity excavation by red-cockaded woodpeckers. This volume.
Harlow, R. F., and M. R. Lennartz. 1983. Interspecific competition for red-cockaded woodpecker cavities during the nesting season in South Carolina. Pages 41-43 *in* D. A. Wood, ed. Red-cockaded woodpecker symposium II proceedings. Fla. Game and Fresh Water Fish Commiss. Tallahassee, Fl.
Hedrick, L. D., R. G. Hooper, D. L. Krusac, and J. M. Dabney. 1998. Silvicultural systems and red-cockaded woodpecker management: another perspective. Wildl. Soc. Bull. 26:138-147.
Hess, C. A., and R. Costa. 1995. Augmentation from the Apalachicola National Forest: the development of a new management technique. Pages 385-388 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tx.
Hovis, J. A., and R. F. Labisky. 1985. Vegetative associations of red-cockaded woodpecker colonies in Florida. Wildl. Soc. Bull. 13:307-314.
Jackson, J. A. 1974. Gray rat snakes versus red-cockaded woodpeckers: predator-prey adaptations. Auk 91:342-347.
Jackson, J. A. 1978a. Analysis of the distribution and population status of the red-cockaded woodpecker. Pages 101-110 *in* R. R. Odum and L. Landers, eds. Proc. rare

and endangered wildlife symposium . Georgia Dept. Nat. Resour., Game and Fish Div. Tech. Bull. W44.

Jackson, J. A. 1978b. Predation by a gray rat snake on red-cockaded woodpecker nestlings. Bird-banding 49:187-188.

Jackson, J. A., M. R. Lennartz, and R. G. Hooper. 1979. Tree age and cavity initiation by red-cockaded woodpeckers. J. For. 77:102-103

James, F. C. 1995. The status of the red-cockaded woodpecker in 1990 and the prospect for recovery. Pages 439-451 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tx.

James, F. C., C.A. Hess, and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecol. Appl. 7:118-129.

James, F. C., C. A. Hess, and B. C. Kicklighter. 2001. Ecosystem management and the niche gestalt of the red-cockaded woodpecker. Ecol. Appl. 11:854-870.

Kappes, J. J., Jr. 1997 Defining cavity-associated interactions between red-cockaded Woodpeckers and other cavity-dependent species: interspecific competition or cavity kleptoparasitism. Auk 114:778-780.

LaBranche, M. S., and J. R. Walters. 1994. Patterns of mortality in nests of Red-cockaded woodpeckers in the sandhills of southcentral North Carolina. Wilson Bull. 106:258-271.

Laves, K. S., and S. C. Loeb. 1999. Effects of southern flying squirrels *Glaucomys volans* on red-cockaded woodpecker *Picoides borealis* reproductive success. Animal Conserv. 2:295-303.

Lennartz, M. R., and D. G. Heckel. 1987 Population dynamcs of a red-cockaded woodpecker population in Georgia piedmont loblolly pine habitat. Pages 48-55 *in* R. R. Odum, K. A. Riddleberger, and J. C. Ozier, eds. Proc. third southeastern nongame and endangered wildl. symposium. Georgia Dept. Nat. Resour., Game and Fish Div., Atlanta.

Ligon, J. D. 1970. Behavior and breeding biology of the red-cockaded woodpecker. Auk 87:255-278.

Ligon, J. D. 1999. The evolution of avian breeding systems. Oxford University Press, Inc., New York, NY. 504 pp.

Loeb, S. C. 1993. Use and selection of red-cockaded woodpecker cavities by southern flying squirrels. J. Wildl. Manage. 57:329-335.

Loeb, S. C., and R. G. Hooper. 1997. An experimental test of interspecific competition for red-cockaded woodpecker cavities. J. Wildl. Manage. 61:1268-1280.

Loeb, S. C., W. D. Pepper, and A. T. Doyle. 1992. Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. South. J. Appl. For. 16:120-125.

Mitchell, L. R., L. D. Carlile, and C. R. Chandler. 1999. Effects of southern flying squirrels on nest success of red-cockaded woodpeckers. J. Wildl. Manage. 63:538-545.

Montague, W. G., J. C. Neal, J. E. Johnson, and D. A. James. 1995. Techniques for excluding southern flying squirrels from cavities of red-cockaded woodpeckers. Pages 401-409 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tx.

Neal, J. C., W. G. Montague, and D. A. James. 1993. Climbing by black rat snakes on cavity trees of red-cockaded woodpeckers. Wildl. Soc. Bull. 21:160-165.

Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Am. Nat. 131:491-525.

Poirier, J., C. Hedman, and M. Register. 2003. Southern flying squirrel use of artificial cavities at International Paper's Southland Forest: the past, present, and future *in* R. Costa and S.J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, WA. In press.

Rudolph, D. C., and S.J. Burgdorf. 1997. Timber rattlesnakes and Louisiana pine snakes: hypotheses of decline. Texas J. Sci. 49:111-122.

Rudolph, D. C., and R. N. Conner. 1991. Cavity tree selection by red-cockaded Woodpeckers in relation to tree age. Wilson Bull. 103:458-467.

Rudolph, D. C., and R. N. Conner. 1994. Forest fragmentation and Red-cockaded woodpecker populations: an analysis at intermediate scale. J. Field Ornithol. 65:365-375.

Rudolph, D. C., and R. N. Conner. 1996. Red-cockaded woodpeckers and silvicultural practice: is uneven-aged silviculture preferable to even-aged? Wildl. Soc. Bull. 24:330-333.

Rudolph, D. C., R. N. Conner, and R. R. Schaefer. 2002. Red-cockaded woodpecker foraging behavior in relation to midstory vegetation. Wilson Bull. 114:235-242

Rudolph, D. C., R. N. Conner, and J. Turner. 1990a. Competition for red-cockaded woodpecker roost and nest cavities: effects of resin age and entrance diameter. Wilson Bull. 102:23-36.

Rudolph, D. C., H. Kyle, and R. N. Conner. 1990b. Red-cockaded woodpeckers vs rat snakes: the effectiveness of the resin barrier. Wilson Bull. 102:14-22.

Rudolph, D. C., R. N. Conner, D. K. Carrie, and R. R. Schaefer. 1992. Experimental reintroduction of red-cockaded woodpeckers. Auk 109:914-916.

Rudolph, D. C., R. N. Conner, R. R. Schaefer, D. Saenz, D. K. Carrie, N. R. Carrie, R. W. Maxey, W. G. Montague, J. Neal, K. R. Moore, J. Skeen, and J.A. Reid. 2003. Red-cockaded woodpecker status and management: West Gulf Coastal Plain and Interior Highlands. This volume

Saenz, D, C. S. Collins, and R. N. Conner. 1998a. A bark-shaving technique to deter rat snakes from climbing red-cockaded woodpecker cavity trees. Wildl. Soc. Bull. 27:1069-1073.

Saenz, D., R. N. Conner, C. E. Shackelford, and D. C. Rudolph. 1998b. Pileated Woodpecker damage to red-cockaded woodpecker cavity trees in eastern Texas. Wilson Bull. 110:362-367

Saenz, D., R. N. Conner, D. C. Rudolph, and R. T. Engstrom. 2001. Is a "hands off" approach appropriate for red-cockaded woodpecker conservation in twenty-first-century landscapes? Wildl. Soc. Bull. 29:956-966.

Skorupa, J. P. 1979. Foraging ecology of the red-cockaded woodpecker in South Carolina.. M.S. Thesis, Univ. California, Davis. 96pp.

Stangel, P. W., M. R. Lennartz, and M. H. Smith. 1992. Genetic variation and population structure of red-cockaded woodpeckers. Conserv. Biol. 6:283-292.

Stober, J. A., and S. B. Jack. 2003. Cleaving Adam's rib: red-cockaded woodpecker restoration on Ichauway *in* R. Costa and S.J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, WA. In press.

Taylor, B. T., and J. R. Walters. 2003. Arthropod communities: a possible link between fire history and red-cockaded woodpeckers *in* R. Costa and S.J. Daniels, eds. Red-cockaded woodpecker: road to recovery. Hancock House Publishers, Blaine, WA. In press.

U. S. Fish and Wildlife Service. 2003. Red-cockaded woodpecker (*Picoides borealis*) recovery plan: second revision. U. S. Fish and Wildlife Service, Atlanta, GA. 296 pp.

Wahlenberg, W. G. 1946. Longleaf pine – its use, ecology, regeneration, protection, growth, and management. C. Lathrop Pack Forestry Foundation. Washington, D. C. 429pp.

Wahlenberg, W. G. 1960. Loblolly pine: its use, ecology, regeneration, protection, growth and management. Duke Univ. School of Forestry. Durham, North Carolina. 603pp.

Walters, J. R. 1990. Red-cockaded woodpeckers: a 'primitive' cooperative breeder. Pages 67-101 *in* P. B. Stacey, and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge Univ. Press, Cambridge, U.K.

Walters, J. R. 2003. Unusual dynamics in a rapidly increasing population of red-cockaded woodpeckers at Camp Lejeune, North Carolina. This volume

Walters, J. R., P. D. Doerr, and J. H. Carter III. 1988. The cooperative breeding system of the red-cockaded woodpecker. Ethology 78:275-305.

Walters, J. R., C. K. Copeyon, and J. H. Carter III. 1992. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. Auk 109:90-97.

Walters, J. R., S.J. Daniels, J. H. Carter III, and P. D. Doerr. 2002a. Defining quality of red-cockaded woodpecker foraging habitat based on habitat use and fitness. J. Wildl. Manage. In press

Walters, J. R., L. B. Crowder, and J. A. Priddy. 2002b. Population viability analysis for red-cockaded woodpeckers using an individual-based model. Ecol. Appl. 12:249-260.

Watson, J. C., R. G. Hooper, D. L. Carlson, W. E. Taylor, and T. E. Milling. 1995. Restoration of the red-cockaded woodpecker population on the Francis Marion National Forest: three years post Hugo. Pages 172-182 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tx.

Weigl, P. D., M. A. Steele, L. J. Sherman, J. C. Ha, and T. L. Sharpe. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the southeast. Bull. Tall Timbers Res. Station No. 24.

Withgott, J. H., J. C. Neal, and W. G. Montegue. 1995. A technique to deter climbing by rat snakes on cavity trees of red-cockaded woodpeckers. Pages 394-200 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, editors. Red-cockaded woodpecker: Recovery, Ecology and Management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State Univ. Nacogdoches, Tx.

Wood, D. A. 1983. Foraging and colony habitat characteristics of the red-cockaded woodpecker in Oklahoma. Pages 51-58 *in* D. A. Wood, ed. Red-cockaded woodpecker symposium II proceedings. Fla. Game and Fresh Water Fish Commiss. Tallahassee, Fl.

Wood, D. A., and J. C. Lewis. 1977. Status of the red-cockaded woodpecker in Oklahoma. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 31:276-282.

Zwicker, S., and J. R. Walters. 1999. Selection of pines for foraging by red-cockaded woodpeckers. J. Wildl. Manage. 63:843-852.