**CURRENT AND FUTURE DYNAMICS OF THE RED-COCKADED WOODPECKER
POPULATION INHABITING THE SAVANNAH RIVER NATIONAL
ENVIRONMENTAL RESEARCH PARK: MANAGING FOR POPULATION GROWTH**

Project Final Report

Submitted by

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INTRODUCTION

The red-cockaded woodpecker was once a common species in the pine forests that dominated the Coastal Plain and much of the Piedmont in the Southeastern United States. Its precipitous decline to endangered status can be attributed to habitat loss and habitat alteration, especially loss of longleaf pine, its preferred habitat, and alteration due to fire exclusion and logging of old growth (USFWS 1985; Ligon et al. 1986; Jackson 1986; 1994; Walters 1990; 1991; Conner et al. 2001). The red-cockaded woodpecker requires old growth because it is the only species of woodpecker to excavate cavities exclusively in the trunks of living pines, and only old trees contain sufficient heartwood to house a cavity. The adverse impact of fire suppression can also be related to cavities. The birds abandon their cavities when hardwood midstory that develops in the absence of fire encroaches on them (Jackson 1978; Van Balen and Doerr 1978; Conner and Rudolph 1989; Costa and Escano 1989). This presumably is because the hardwoods provide predators the means to circumvent the pine resin barrier the birds create around their cavities.

Red-cockaded woodpeckers also are unusual in exhibiting a cooperative breeding system (Brown 1987). In such systems some adult individuals, called helpers, assist others in raising offspring rather than reproducing themselves. In red-cockaded woodpeckers, most helpers are previous male offspring of the breeding pair (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988; Walters 1990). Helpers become breeders by inheriting a breeding position on their natal territory, or dispersing to fill a vacancy on a neighboring one (Walters et al. 1988; 1992a). Offspring that do not remain as helpers, which include some males and most females, disperse within the first year. Dispersing young may move long distances, although most move only a few territories from their natal site (Walters et al. 1988; 1992a; Daniels 1997; Daniels and Walters 2000). Age-specific fecundity and mortality rates, plus a rate of status transition from fledgling to breeder, are sufficient to describe the population dynamics of most avian species. Because of the cooperative breeding system, the population dynamics of red-cockaded woodpeckers are more complex, and require in addition status transitions from fledgling to helper and helper to breeder (Heppell et al. 1994; Maguire et al. 1995; Letcher et al. 1998).

The adaptations of cooperative breeding and excavating cavities in pines are closely related, and this relationship is fundamental to population behavior. Cavities take many years to excavate (Conner and Rudolph 1995; Harding 1997), and are used for roosting and nesting for an equally long period once completed. The sets of cavities found on territories thus constitute an extremely valuable resource, and the population dynamics of the species revolve around them. Generally, cooperative breeding is thought to evolve under conditions of high variability in territory quality (Koenig and Pitelka 1981; Stacey and Ligon 1991; Emlen 1991; Koenig et al. 1992). Under these conditions, it is advantageous for individuals to remain at home and await a breeding vacancy on a high quality territory in the vicinity, rather than dispersing to wander in search of a vacant territory, which may well be a poor quality one. In the red-cockaded woodpecker territories with existing cavities are the high quality ones, and those that contain all other resources but lack suitable cavities are the poor quality ones (Walters 1991; Walters et al. 1992b). Habitat without cavities is rarely occupied, whereas the birds compete intensely over areas with cavities, and will move into those lacking them when artificial cavities are added (Copeyon et al. 1991; Walters et al. 1992b).

Naturally, new territories form by two processes, budding and pioneering (Hooper 1983). Budding involves the splitting of one territory, and its cluster of cavity trees, into two. Budding is initiated by a helper male from the original territory, or by an intruding male dispersing from

elsewhere. The new budded territory contains some previously existing cavities wrested from the original group, but often a new cavity is excavated some distance from the original cavity tree cluster as well. Pioneering involves the colonization of unoccupied habitat lacking preexisting cavities, and thus always involves the excavation of new cavities. Pioneering invariably is initiated by a dispersing male. Population growth due to budding is ten times as high as growth due to pioneering in most populations (1-2% per year vs. 0.1-0.3% per year, Conner et al. 2001). Providing cavities in unoccupied habitat (i.e., construction of recruitment clusters) typically increases population growth through new territory formation by an order of magnitude, i.e., to 10% per year (Conner et al. 2001). This is because the process by which recruitment clusters are occupied resembles breeder replacement on existing territories rather than pioneering. Thus either helper males from neighboring groups or dispersing male fledglings may occupy a recruitment cluster (Walters et al. 1992b).

A management strategy for recovering red-cockaded woodpecker populations has been derived from the understanding of population dynamics just described. This strategy focuses on preventing abandonment of existing territories and creating new ones, rather than on increasing survival or reproduction (Walters 1991). Specific management techniques have been developed with this view of population dynamics in mind. Cavity restrictors (Carter et al. 1989) are designed to reduce territory abandonment by protecting cavities from other species. Construction of artificial cavities (Copeyon 1990; Allen 1991; Copeyon et al. 1991) can be used both to maintain territory quality by providing replacement cavities and to stimulate population growth through creation of recruitment clusters. Growing season fire can be used to reduce hardwood midstory, and thereby reduce territory abandonment (Frost et al. 1986; Ware et al. 1993). Juvenile birds can be translocated within or between populations to stimulate occupation of recruitment clusters (DeFazio et al. 1987; Rudolph et al. 1992; Allen et al. 1993).

This management strategy has been highly successful. Prior to its widespread adoption in the early 1990s, only one red-cockaded woodpecker population was reported to be increasing (Hooper et al. 1991), and most were declining. Now many populations are increasing under this management regime, although the several populations in which such management is not employed continue to decline or, at best, remain stable (Conner et al. 2001). Nowhere has the reversal of population behavior under new management been more dramatic than at the Savannah River Site (SRS) in South Carolina.

Red-cockaded Woodpeckers at the Savannah River Site

The recent history of the red-cockaded woodpecker (*Picoides borealis*) population inhabiting SRS represents one of the most spectacular success stories in endangered species management (Franzreb 1997). Longleaf pine forests dominated SRS historically (Frost 1997, in Edwards et al. 1998). As in many other areas, much of this habitat was converted to other pine forest types, and what longleaf forest remained was greatly altered by virtual elimination of old growth and development of hardwood midstory due to fire suppression (White 1997). Hence the decline of the red-cockaded woodpecker population on SRS that accompanied these habitat changes, like most declines, can readily be related to territory loss. The population at SRS declined to the brink of extinction: in December 1985, the population consisted of only four birds, one breeding pair and two solitary males (Jackson 1990).

Managers at SRS responded to this critical situation with intensive management that included elements of the new management strategy described above and some additional measures. They made extensive use of prescribed fire and other methods to control hardwood

midstory, constructed artificial cavities to rehabilitate existing territories and create new recruitment clusters, and translocated individuals from other populations (Edwards et al. 1998). In addition, managers employed various means to protect cavities and nests from the southern flying squirrel (*Glaucomys volans*) and other cavity kleptoparasites (Kappes 1997) and nest predators (Edwards et al. 1998). Under this management regime, the SRS population by 1995 had increased to 20 breeding groups and thus was rescued from oblivion (Franzreb 1997). Most new groups were on territories created or rehabilitated through artificial cavity construction, and many of the individuals occupying these sites were captured in other populations, especially from the Apalachicola National Forest in Florida, and released at SRS (Haig et al. 1993; Edwards et al. 1998).

The intensive management of the late 1980s and early 1990s, although necessary to rescue the population from extinction, cannot continue indefinitely for two reasons. First, as the population grows, the human and fiscal resources required for this level of management become increasingly prohibitive, and their cost effectiveness increasingly questionable. Second, this style of management became less successful as the population expanded. Whereas the population increased by 19 groups between 1985 and 1995, between 1995 and 1997 it grew by only two additional groups (Edwards et al. 1998). Early population growth was no doubt dependent on the individual attention each territory, and each bird, received. Continued population growth will require a greater contribution from the natural dynamics of the population, and less reliance on human intervention. The issue SRS now faces is how to more effectively make use of natural population processes in managing for population growth.

The problem confronting SRS is a general one. Many populations of red-cockaded woodpeckers currently are of similar, small size, and are far smaller than the population objective set for their management unit (James 1995). Devising a means to increase such populations efficiently is a major research and management issue. Populations of larger size at Camp Lejeune in North Carolina (30 groups), Croatan National Forest in North Carolina (45 groups) and Eglin Air Force Base in Florida (200 groups) have increased at the rate of 10% per year under less intensive management than previously practiced at SRS (Conner et al. 2001). At these sites, growth has resulted from natural dispersal to recruitment clusters created within landscapes that are managed to provide suitable habitat.

The purpose of this study was to evaluate the potential for a similar management strategy to promote population growth at SRS. The management effort required would be much less than the current level, as desired, but the viability of this strategy at SRS is unclear because the density and number of woodpecker groups are significantly reduced compared to the sites where the strategy has been successful previously. Specifically we analyzed the observed dynamics of the population and explored future dynamics through simulation modeling in order to assess the potential for population growth through natural dispersal to recruitment clusters at SRS. We attempted to determine what has limited population growth in the past few years, as well as assess the potential for growth in future years.

OBJECTIVES

The study includes three specific objectives. First, the dynamics of the SRS population are described and compared to those of other populations to identify factors limiting population growth currently. Dispersal rates are especially emphasized in this exercise. Second, recruitment clusters are evaluated to determine what properties of individual cavity trees, surrounding habitat, and the surrounding landscape may limit occupancy through natural

dispersal. Third, a spatially-explicit, individual-based simulation model is used to project expected dispersal rates and population growth under current conditions, and compare those estimates to observed dispersal and population growth. The model also is used to explore how placement of recruitment clusters and managing to increase productivity might contribute to population growth.

DESCRIPTION OF POPULATION DYNAMICS

The goal of this portion of the proposed research is to describe the current dynamics of the SRS population and compare them to those of other, well-studied populations in order to identify possible limitations on population growth. To accomplish this we calculated mortality rates, reproductive rates and status transition probabilities using data previously collected at SRS and compared them to values from four other populations we study. These are the North Carolina Sandhills (data from 184-218 groups per year for 19 years, 1980-1998), Camp Lejeune (data from 28-46 groups per year for 13 years, 1986-1998), Croatan National Forest (data from 38-56 groups per year for 9 years, 1989-1997) and Eglin Air Force Base (data from 100 groups per year for 7 years, 1992-1998) populations. Originally we planned to calculate parameter values for two periods at SRS, (1) the period of rapid population increase (1986-1994) and (2) the period of relatively little population growth (1995-1998). However, the parameter values for the first period turned out to be rather meaningless because so many birds were imported from other populations during this period, and because so many birds were translocated to recruitment clusters. Therefore we will limit our analysis of the SRS data to 1995-1998.

Survival rates (Table 1) and reproductive rates (Table 2) at SRS compare favorably to those in other populations. The pattern of geographic variation in these parameters in red-cockaded woodpeckers is that survival rates tend to be higher and reproductive rates lower in more southern and more coastal populations (Conner et al. 2001). Thus one expects survival to be higher and productivity lower at SRS compared to the other, more northern inland population in the Sandhills, and comparable to the more northern, but coastal Camp Lejeune and Croatan populations. Further, one expects productivity to be higher than in the Eglin population located in coastal Florida. Values for fledgling survival at SRS match the expected pattern, but survival of adults is somewhat higher than anticipated (Table 1). More significantly, productivity is considerably higher than anticipated (Table 2). Note that survival rates of fledgling females and helper males seem somewhat depressed compared to other survival rates at SRS (Table 1). This relates to dispersal patterns discussed below.

Table 1. Annual survival rates of red-cockaded woodpeckers in four populations. Survival is calculated as the proportion of individuals alive in one breeding season resighted the next breeding season. Survival rates could not be calculated for Eglin because not all groups in this population were monitored.

	Savannah River	Sandhills	Camp Lejeune	Croatan
Fledgling male	57%	50%	59%	46%
Fledgling female	34%	42%	43%	36%
Breeding female	83%	71%	77%	75%
Breeding male	92%	76%	82%	80%
Helper male	80%	83%	78%	78%

Table 2. Reproductive parameters from five red-cockaded woodpecker populations. Values are means (ranges in parentheses) among years. Parameters are described in the text below.

	Savannah River	Sandhills	Camp Lejeune	Croatan	Eglin
% groups nest	98 (92-100)	83 (75-96)	89 (79-100)	89 (84-93)	92 (85-98)
Clutch size	3.4 (2.9-3.7)	3.2 (3.2-3.5)	3.4 (3.1-3.8)	3.3 (3.2-3.6)	3.2 (3.0-3.4)
Whole brood loss	25% (18-32)	23% (14-28)	19% (8-32)	23% (12-32)	26% (19-30)
Partial brood loss	29% (18-40)	35% (33-43)	43% (33-54)	41% (31-49)	46% (39-51)
Brood size	2.4 (2.1-2.4)	2.1 (1.9-2.3)	2.0 (1.6-2.2)	2.0 (1.6-2.3)	1.8 (1.6-1.9)
Fledglings / group	1.9 (1.6-2.3)	1.4 (1.2-1.7)	1.5 (1.0-2.0)	1.4 (1.1-1.6)	1.3 (1.2-1.6)

The high productivity at SRS, measured as the number of fledglings produced per group, is due to the combination of the high proportion of groups that nest and large brood sizes, measured as the number of fledglings from successful nests (Table 2). Large brood sizes result from unusually low rates of partial brood loss (measured as the percentage of eggs that result in fledglings in successful nests) rather than unusually large clutch sizes. Whole brood loss (measured as the percentage of nests that fail), in contrast to partial brood loss, is fairly high at SRS. That a high proportion of groups nest at SRS might be attributable to protection of cavities from kleptoparasites, but it might also be due to unusually good conditions for breeding. Low rates of partial brood loss and high rates of whole brood loss are more consistent with the latter than the former. Why conditions for breeding should be unusually good at SRS is a mystery. Factors associated with high rates of productivity elsewhere, namely large numbers of helpers (Walters 1990) and availability of large old trees and a rich ground cover in foraging areas (James et al. 1997; 2001; Hardesty et al. 1997; Walters et al. in review), are lacking at SRS compared to the other populations evaluated. Further investigation of the factors responsible for high rates of survival and productivity at SRS may yield new insights into the demography of red-cockaded woodpeckers. Whatever these factors may be, it is clear that survival rates and productivity are not limiting population growth at SRS.

Instead, it appears that low rates of transition from nonbreeding to breeding status due to low dispersal success are limiting population growth. That dispersal success of nonbreeders is poor at SRS relative to other populations is evident from comparisons of annual transition probabilities. Relatively many male fledglings remain on their natal territories as helpers at SRS, but relatively few helpers are able to acquire breeding positions each year (Table 3). A relatively large number of female fledglings remain as helpers as well, but very few female fledglings are able to disperse and find a breeding position in their first year (Table 3). The difficulty female fledglings and male helpers have finding a breeding position is due in part to the high survival rates of breeders, and resulting low turnover in breeding positions on existing territories. However, the large number of unoccupied recruitment clusters available at SRS more than compensates for the low number of vacancies on existing territories. Indeed, male fledglings are unusually successful in dispersing and acquiring territories in their first year at SRS (Table 3), and the territories they acquire usually are recruitment clusters. This cannot be attributed to translocation, as translocated birds were excluded from the analyses. Instead, the success of these young males likely is due to the fact that fledgling males tend to disperse long distances and wander rather widely. Fledgling females do not move as far as fledgling males, and dispersal of helpers is restricted to their immediate neighborhood (Walters et al. 1988; Daniels 1997; Daniels and Walters 2000). Hence it appears that it is difficult for individuals to find

breeding vacancies in close proximity to their home territory at SRS, and this is having negative effects on those classes of individuals that rely on short-distance dispersal, namely helper males and fledgling females.

Table 3. Annual status transition probabilities from four red-cockaded woodpecker populations. Transition probabilities are the percentage of individuals in the first status class in year 1 that are alive and in the second status class in year 2. Transition rates could not be calculated for Eglin because not all groups in this population were monitored.

	Savannah River	Sandhills	Camp Lejeune	Croatan
Females				
Fledgling to Helper	9%	1%	8%	3%
Fledgling to Breeder	14%	29%	18%	23%
Males				
Fledgling to Helper	37%	27%	43%	28%
Fledgling to Breeder	6%	5%	2%	3%
Fledgling to Solitary Male	8%	4%	2%	3%
Helper to Breeder	9%	27%	19%	19%

Simulation modeling, as well as empirical work, indicates that the spatial distribution of territories has a strong effect on population stability, and that this effect is due to the behavior of helpers (Letcher et al. 1998; Walters et al. 2001). Helpers, by serving as a pool of replacement breeders, buffer effects of variation in mortality and productivity on population size. When mortality of breeders is high and productivity low, the number of breeding pairs does not decline. Instead, more helpers become breeders. Thus it is the size of the helper class rather than the size of the breeding class that fluctuates. But this buffering effect only occurs when territories are aggregated, because helpers disperse only short distances. Apparently helpers monitor their own and neighboring territories, and simply wait until a breeding vacancy arises on one of them. They are unaware of, and incapable of filling, breeding vacancies outside their neighborhood (Walters et al. 1988; Daniels 1997). Similar principles apply to helper contributions to population growth through occupation of recruitment clusters. Helpers represent a pool of potential occupants of recruitment clusters and thus are expected to stimulate population growth, but only when suitable recruitment clusters are aggregated with existing territories. Lack of population growth, coupled with low rates of transition from helper to breeder status, suggests that either recruitment clusters are not in close enough proximity to existing territories or they are not acceptable to the birds.

Females generally will not occupy recruitment clusters unless a male is already present. Hence the poor dispersal success of fledgling females may be due to the failure of helper males to occupy recruitment clusters, coupled with low turnover on existing territories. However, fledgling males that are able to locate recruitment clusters often remain unpaired, suggesting that fledgling females either are having difficulty locating recruitment clusters or find the recruitment clusters or the young males occupying them unacceptable. That females might have difficulty locating recruitment clusters is somewhat surprising, since fledgling females sometimes disperse considerable distances (Daniels and Walters 2000). The average natal dispersal distances of red-cockaded woodpeckers, however, are among the shortest documented for any bird species (Daniels and Walters 2000). Dispersal of fledglings females, although not as restricted as that of

male helpers, may also be geared toward short-distance movements. Therefore dispersal success of fledgling females might also be negatively affected by a poor spatial distribution of territories.

The results of the first portion of our research thus suggest that population growth at SRS is limited either by over-dispersion of recruitment clusters and existing territories or by poor quality of recruitment clusters. The management solution to this problem is either strategic placement of recruitment clusters to improve spatial aggregation of territories or improving quality of recruitment clusters. Our results further suggest that other management actions aimed at other aspects of population dynamics, such as increased nest protection to improve reproduction or increased construction of artificial cavities in existing territories to improve survival, will be relatively ineffective in stimulating population growth.

ANALYSIS OF ARTIFICIAL CAVITY SITES

The first portion of the research suggests the possibility that previous population growth at SRS might reflect occupation of the best and most easily located recruitment clusters, and once these were occupied, growth slowed because the remaining sites were less attractive or less likely to be found. The second portion of the research provides additional assessment of this possibility. The goal of this portion of the research is to determine what properties of recruitment clusters might limit their occupancy through natural dispersal. As part of this work, we attempt to distinguish the two possibilities identified in the first portion of the research, poor quality and poor spatial distribution of recruitment clusters.

Rather than measure all imaginable features of cavity trees, habitat and the surrounding landscape for each recruitment cluster, we relied on a concurrent study to identify potentially important variables. Ms. Nicole Chadwick, a graduate student working with us at Virginia Tech, analyzed occupancy of 78 recruitment clusters on Eglin Air Force Base in Florida. She examined properties of cavities such as height, orientation and dimensions, properties of cavity trees such as tree age, tree size, sapwood thickness and sap flow, properties of the surrounding habitat such as pine type, pine density, snag density, hardwood midstory development and ground cover, and properties of the surrounding landscape such as local density of existing groups, proportion of unsuitable habitat in the landscape, and fragmentation of pine habitat.

Chadwick (2001) determined that on Eglin recruitment clusters with higher cavities, cavity trees with higher resin flow, richer groundcover (i.e., more wiregrass, forbs, vines and hardwood stems and less bare ground) and more existing groups within 2 km were more likely to be occupied. Cavity height, resin flow and groundcover are features of site quality, whereas the number of groups within 2 km is a feature of spatial distribution. Cavity height is unlikely to be an issue at SRS, as the low cavities (i.e., 3-5 m in height) that negatively affected occupancy on Eglin are not present on SRS. Because Chadwick's results were not available until recently (Chadwick 2001), we did not have the opportunity to evaluate the quality of recruitment clusters at SRS by measuring ground cover and resin flow. Although we believe it is spatial distribution of recruitment clusters rather than their quality that is limiting their occupancy at SRS (see below), it may still be worthwhile to measure resin flow and groundcover to determine whether site quality may be an issue for at least a few of the unoccupied recruitment clusters at SRS, especially those that are in reasonable proximity to existing territories (see below).

We did examine spatial distribution, and determined that this is very likely to be limiting occupancy of recruitment clusters at SRS. Of 11 recruitment clusters constructed prior to 1995 that had more than two active clusters within 2 km of them, 6 (55%) have been occupied, whereas only 5 of 16 (31%) that had two or fewer active clusters within 2 km have been

occupied. This difference is not statistically significant (X^2 test, $p < 0.3$) but is suggestive given that birds were translocated to many recruitment clusters, thus reducing any impact of cluster isolation. Of the 28 recruitment clusters constructed from 1995 to 1998, only one had as many as three active clusters within 2 km, and 25 had none. Thus lack of occupancy of recruitment clusters through natural dispersal in recent years is consistent with the hypothesis that recruitment clusters and existing territories are not sufficiently aggregated. Other data suggest that spatial isolation is an issue at SRS. Combining natural and recruitment clusters, in 1995 the distance to the nearest active cluster was significantly less for active clusters (mean = 991 m, $n = 16$) than for inactive clusters (mean = 3810 m, $n = 54$) (t-test, $p < 0.0001$).

The relatively scattered distribution of unoccupied recruitment clusters at SRS is readily apparent (Figures 1 and 2). Because those that are not within 2 km of any existing groups may be too isolated to be efficiently occupied through natural dispersal, we do not recommend expending effort to evaluate their quality, or to improve or maintain them. We do recommend measuring resin flow and groundcover to assess the quality of recruitment clusters within 2 km of existing groups and taking management action to correct any deficiencies in quality identified. For example, if all trees in a particular site are deficient in sap flow, that site might be improved substantially by constructing cavities in trees with high sap flow, or if groundcover is poor, it might be improved using growing season fire. Finally, we recommend that any additional recruitment clusters constructed be placed within 2 km of three or more active clusters.

Thus the second portion of the research supports the first in providing further evidence that population growth at SRS is limited by the inability of nonbreeders, specifically helper males and fledgling females, to successfully disperse to recruitment clusters because recruitment clusters and existing territories are not sufficiently aggregated. We explore this theme further through simulation modeling in the third and final portion of the research.

SIMULATION MODELING

In the third portion of the research, we employ a spatially-explicit, individual-based simulation model to project expected dispersal rates and population growth under current conditions, and compare those estimates to observed dispersal and population growth. We also use the model to examine how placement of recruitment clusters might affect population growth. Thus we explore the effects of spatial distribution of existing territories and recruitment clusters on population dynamics identified in the first two portions of the study.

Simulation modeling can be a valuable tool for projecting future population behavior. Typically matrix models are used in population viability analyses to project population dynamics over long periods of time (Beissinger and Westphal 1998). Stage-based matrix models have been used to gain insight into population dynamics and the importance of certain vital rates (i.e., mortality rates, reproductive rates, status transition probabilities) to population behavior in red-cockaded woodpeckers (Heppell et al. 1994; Maguire et al. 1995). However, matrix models cannot accurately simulate population dynamics of red-cockaded woodpeckers, because they cannot incorporate spatial constraints on helper dispersal (see above).

Spatially-explicit, individual-based models, because they track the performance and fate of individual organisms (Judson 1994) and their locations (Dunning et al. 1995), can incorporate constraints on movement. In these simulation models, population dynamics are the summation of what happens to the individuals in the population. A major limitation of these complex models is the amount of data required for parameter estimation (Murdoch et al. 1992; Conroy et al. 1995; Beissinger and Westphal 1998). Fortunately, extensive, detailed demographic data for

red-cockaded woodpeckers are available from the North Carolina Sandhills (Carter et al. 1983; Walters et al. 1988; Daniels 1997). Previously we used these data to construct a spatially-explicit, individual-based population model for red-cockaded woodpeckers (Letcher et al. 1998). To a large extent, the data drove construction of the model, and dictated its structure.

Figure 1. Distribution of active clusters (closed circles) and inactive recruitment clusters (open circles) on northern SRS in 1998. Only a few recruitment clusters are in close proximity (i.e., < 2 km) to a number of active clusters.

The model is described in detail in Letcher et al. (1998). Briefly, the landscape in the model consists of breeding territories and non-breeding space that the birds must cross to find territories. Territory locations are fixed, but territories are lost if unoccupied for more than five consecutive years. New territories arise through budding, and each existing territory has a 1% probability of producing a bud each year. The model is configured for both males and females, which have different life histories. Female fledglings disperse, whereas male fledglings may either disperse or become helpers. Dispersing fledglings depart in a random direction, and continue in that direction at a specified rate until they die, obtain a breeding position or leave the population. Each time step, they compete for any breeding vacancy within 3 km of their current position. Males may compete for both breeding vacancies and empty territories, but females may only move into territories that contain a male. Helpers do not change status or location until

they die or fill a breeding vacancy. The oldest helper inherits breeding status if the same-sex breeder on its territory dies, and helpers compete for any breeding vacancies within 3 km of their home territory. The probability of mortality of each individual depends on its status, and the number of fledglings produced on each territory each breeding season is a function of breeder age and number of helpers present. In this species young birds (i.e., < age 4) are less productive than older ones (Walters et al. 1988; 1992a; Walters 1990) and helpers increase the productivity of their group (Lennartz et al. 1987; Walters 1990; Heppell et al. 1994).

Figure 2. Distribution of active clusters (closed circles) and inactive recruitment clusters (open circles) on southern SRS in 1998. Only a few recruitment clusters are in close proximity (i.e., < 2 km) to a number of active clusters.

Simulation of the 1995 SRS Population

The model can be applied to real populations, provided all territory locations are known. In the first simulation exercise, we applied the model to the SRS population, using the actual population in 1995 as the initial population. Unoccupied recruitment clusters were included as empty territories. The initial population included 17 occupied territories and 33 unoccupied recruitment clusters. The simulation was run for 20 years and was replicated 100 times. We evaluated population growth, measured in terms of occupied territories, and also the probability that each unoccupied recruitment cluster would be occupied (measured as the proportion of 100 replicates in which the site was occupied). Our goal in conducting this exercise was to determine

whether the recent decrease in population growth rate is expected given the current size and spatial configuration of the population. This simulation projects expected population behavior in the absence of further management beyond maintaining suitable habitat.

Our simulations of the current population project a population decline. Although the population became extinct within 20 years in only 4 of the 100 replicate simulations, the average population size at the end of 20 years was quite small (Figure 3). These results reinforce the notion that the current spatial distribution of active clusters and recruitment clusters within the population is not conducive to population growth through natural population dynamics. That is, the simulations suggest that the current population cannot be expected to sustain itself, let alone grow, through natural processes.

Figure 3. Population size, measured in number of occupied territories (i.e., active clusters), over time in simulations of the 1995 Savannah River population. Mean and standard deviation among 100 replicates are shown.

The results of this simulation exercise also support the notion that nonbreeders are unable to locate the existing recruitment clusters efficiently. A few recruitment clusters were occupied in a large proportion (i.e., $\geq 40\%$) of the simulations, but others were not occupied in even a single simulation. The proportion of runs in which a recruitment cluster was occupied was a direct function of its proximity to active territories (Figure 4). Since we assumed that all recruitment clusters were acceptable to the birds, effects of recruitment cluster quality were not a factor in these simulations. Thus these results suggest that the spatial distribution of recruitment clusters is a sufficient explanation of lack of occupancy.

Figure 4. Proportion of 100 replicates in which each of the 33 empty territories (i.e., recruitment clusters) (yellow symbols) was occupied. Blue symbols indicate the initial 17 occupied territories. Note that occupancy is positively related to proximity to active territories.

The poor population performance projected by the modeling indicates that proactive management will be necessary to sustain continued growth of the SRS woodpecker population.

The potential for strategic placement of additional recruitment clusters to satisfy this management need is explored in the next simulation exercise.

Simulation of Recruitment Cluster Placement

In the second simulation exercise we explored the projected impact of recruitment clusters on population growth. In these simulations, we added recruitment clusters to the landscape as empty territories at locations previously identified by SRS personnel as recruitment stand sites. There were 20 such recruitment clusters. Several scenarios were run, differing in the rate at which recruitment clusters were added and in how we selected among recruitment cluster locations. The rates used were 5 sites per year and 2 sites per year, which correspond to initial population growth rates of 25% and 10% per year respectively. In the former case, all the recruitment clusters were added to the landscape in the first 4 years of the 20-year simulation, and in the latter case in the first 10 years. Within each rate, three scenarios were simulated: (1) recruitment clusters were added in random order; (2) recruitment clusters were added in order of proximity to an existing territory; and (3) recruitment clusters within a minimum distance (3 km) to an occupied territory were added in random order. This minimum distance is the maximum dispersal range of helpers in the model. The goal of these simulations was to identify the most effective rate of adding and method of selecting recruitment clusters, in terms of both population growth rate and the proportion of recruitment clusters added that are occupied. Recall that the model labels sites that remain vacant for five years following construction as extinct, and thus they are never occupied.

The results of this simulation exercise were surprising in that population behavior was remarkably similar among the various scenarios. In none of the scenarios did population growth rate exceed the value for the current population (Table 4), although population size at 20 years sometimes did (Figure 5). Variation among treatments in growth rate was small (Table 4), and the average population size at 20 years was 7-8 active territories. On average, only 2 of the 20 recruitment clusters were occupied, regardless of how they were added, and 5 of the 33 existing empty territories were occupied, regardless of whether or not additional recruitment clusters were added (Table 4). We conclude that the number of empty territories is not limiting population growth, and indeed is excessive relative to the size of the existing population. Thus adding more recruitment clusters does not have a beneficial effect.

Table 4. Annual population growth rate, number of new recruitment clusters (of 20) occupied and number of initially empty territories (of 33) occupied under different strategies for adding recruitment clusters. Strategies are described in the text. Values are means among 100 replicate simulations for each strategy, with standard deviations in parentheses.

Strategy	Population Growth Rate	Recruitment Clusters Occupied	Empty Territories Occupied
None	0.944 (0.052)	-	5.48 (2.17)
2/yr, random	0.937 (0.057)	2.34 (1.71)	5.70 (2.13)
2/yr, nearest occupied	0.936 (0.059)	2.14 (1.58)	4.73 (1.92)
2/yr, random within 3 km of occupied	0.937 (0.066)	1.78 (1.37)	5.08 (2.26)
5/yr, random	0.934 (0.057)	1.93 (1.38)	4.98 (1.86)
5/yr, nearest occupied	0.936 (0.060)	1.72 (1.10)	4.80 (2.16)
5/yr, random within 3 km occupied	0.943 (0.059)	1.78 (1.24)	4.84 (2.03)

Figure 5. Number of occupied territories after 20 years as a function of method of adding 20 recruitment clusters. Mean and standard deviation among 100 replicates are shown. Nominal case is the 1995 population (17 active territories + 33 empty territories). Methods differ in rate of addition (2 per year or 5 per year) and how sites are selected (Rand = random; Nearest = in order of proximity to existing territories; 3 km = random among those within 3 km of existing).

As with empty territories, the location of new recruitment clusters had a large effect on the probability that they would be occupied. Those in close proximity to several existing active territories were occupied in a large proportion of the simulations, whereas those distant from existing active territories were never occupied in some scenarios (Figure 6). The distribution of the new recruitment clusters was similar to that of existing empty territories in that many were relatively isolated from existing active territories. In fact, the new recruitment cluster locations tended to be more isolated than the empty territory locations (Figure 6). This presumably was a major factor in their relative ineffectiveness in stimulating population growth.

There was little difference in any measure of success among the different strategies for adding recruitment clusters. Picking only among those within 3 km of occupied territories was more cost-efficient than the others: most of the recruitment clusters that were never occupied under this strategy in fact were never added to the landscape as they never were within 3 km of an occupied territory. Thus this strategy avoided addition of recruitment clusters that had very low probabilities of being occupied. Still, it did not stimulate population growth.

Figure 6. Proportion of 100 replicates in which each of the 20 recruitment clusters (yellow symbols) were occupied. Blue symbols indicate the 17 initially occupied (with dots) and 33 initially empty territories (open circles). Recruitment clusters were added in random order at a rate of two per year.

We conclude that use of the additional recruitment clusters already planned will not improve population dynamics. Additional proactive management will be needed. Possibilities include translocating birds to empty territories and new recruitment clusters and identifying other locations for recruitment clusters that are in much closer proximity to existing active territories. A final possibility, enhancing productivity, is evaluated in the final simulation exercise.

Simulation of Enhanced Productivity

In the first part of this research, we showed that productivity of red-cockaded woodpeckers at SRS is high. Several management techniques currently or previously practiced on SRS represent means to protect cavities or nests, and thereby elevate productivity. Cavity restrictors, SQEDs and flying squirrel removal are examples (Edwards et al. 1998). Laves and Loeb (1999) demonstrated that on SRS flying squirrel removal increases productivity, and other measures may have similar effects. However, these measures are labor-intensive, and their cost-effectiveness is an issue, particularly if productivity is not limiting population growth. To further evaluate the utility of continuing management practices designed to increase productivity, we explored the potential impact of these measures on population growth in the final simulation exercise. We simulated population behavior using two different reproductive rates that represent “normal” reproduction and “enhanced” reproduction. Normal reproduction was represented by the standard model parameters. Productivity was increased by 0.7 fledglings per group, the effect size identified by Laves and Loeb (1999), to represent enhanced reproduction. The population used in this simulation exercise consisted of the 17 active and 33 empty territories present in 1995.

Population dynamics were much improved when productivity was elevated. Population growth rate indicated an increasing population, the mean number of territories occupied after 20 years exceeded the initial number of active territories, and more empty territories were occupied than in any of the previous scenarios (Table 5). The slow population increase projected by the simulations matches the observed behavior of the real population in recent years. As before, the recruitment clusters occupied most often were those closest to existing groups (Figure 7). With more fledglings to locate them, the likelihood that an individual recruitment cluster would be occupied was higher than in previous simulations, with the exception of the most isolated recruitment clusters, which still were never occupied (Figure 7 vs. Figures 4 and 6).

Table 5. Comparison of simulated behavior of the 1995 population with (Normal) and without (Enhanced) enhanced productivity. Means and standard deviations among 100 replicates are given. The initial population was 17 occupied and 33 empty territories.

Parameter	Normal	Enhanced
Growth Rate	0.94 (0.052)	1.03 (0.020)
Number of Occupied Territories After 20 Years	7.54 (4.63)	24.6 (6.81)
Number of Empty Territories Occupied	5.48 (2.17)	8.91 (2.75)

Figure 7. Proportion of 100 replicates in which each of the 33 empty territories (i.e, recruitment clusters) (yellow symbols) was occupied. Blue symbols indicate the initial 17 active territories.

GENERAL DISCUSSION

The consistent theme amidst the various analyses in this study is that the contribution of natural population dynamics to the growth of the red-cockaded woodpecker population at SRS is

limited by poor dispersal success of nonbreeding birds, specifically helper males and fledgling females, due to an unfavorable spatial distribution of recruitment clusters relative to active territories. Although it is possible that some recruitment clusters are unattractive to the birds due to their poor quality, our results indicate that the spatial distribution of recruitment clusters alone can account for poor dispersal success, independent of any effect of site quality. Not only is the population split into disjunct northern and southern subpopulations, but within each subpopulation empty territories (Figure 4) and future recruitment cluster locations (Figure 6) are not sufficiently aggregated with existing territories. It is this problem that limits dispersal success and thus population growth.

The existing territories themselves are fairly well aggregated, at least within subpopulations (Figure 4), and this is reflected in population behavior. In comparing simulation results, it is important to focus on relative differences between simulation scenarios rather than on the actual values obtained. That one population performs better than another is more informative than whether a particular population increased or decreased. Based on such comparisons, we find that the performance of the existing population in simulations is quite good, considering its size. In a previous analysis using this same simulation model, we examined the effects of population size, territory density and level of territory aggregation on the dynamics of hypothetical populations (Walters et al. 2001). Without enhanced productivity, the population growth rate of the SRS population in this study is similar to the highest growth rates of populations of similar size in the previous study, and with enhanced productivity it exceeds those rates. In our previous simulations, the higher growth rates occurred in the populations with the highest population densities and most aggregated territories. This is because the strong stabilizing influence of helpers on population behavior described above depends on territories being close enough together that helpers can readily disperse among them (Walters et al. 2001). Evidently existing territories are sufficiently aggregated that helpers can disperse among them. This lends stability to the existing population, but because breeder survival is so high, opportunities for helpers to become breeders on existing territories are infrequent. Opportunities for helpers to become breeders in recruitment clusters are abundant, but the locations of these clusters prevent helpers from taking advantage of these opportunities.

What appeared to occur in the simulations of the SRS population was that although most empty territories and recruitment clusters remained vacant, those few that were in close proximity to existing territories were occupied. As a result, there was an initial increase in population density and territory aggregation, which improved helper dispersal and thus population dynamics. In many simulations, population size actually increased slightly at first (e.g., Figure 3). Isolated existing territories were soon abandoned, however, and the two aggregations of territories, one in the north and one in the south, proved too small to sustain themselves in the face of environmental and demographic stochasticity.

We conclude that the existing active territories, although well aggregated, are too few to constitute a viable population. Therefore it will continue to be necessary to stimulate population growth through management for the foreseeable future, until the population becomes sufficiently large to be viable. The population exhibits sufficient stability, both empirically and in simulations, that achieving population growth through management is a reasonable goal. This does not appear to be a population that is struggling to persist, but rather, one that is healthy enough to respond positively to management. Previous simulations indicate that if territories are well aggregated, a population of as few as 100 active territories could be viable (Walters et al. 2001). Increasing the population to this level seems to us a realistic goal. However, our results

indicate that because of their spatial distribution, the existing and planned recruitment clusters will not be effective in promoting the necessary population growth through natural dispersal processes. To grow the population, it will be necessary either to accomplish occupation of the existing and planned recruitment clusters through translocation, or to establish new recruitment clusters in more desirable locations near active territories and allow the birds to occupy them through dispersal. We recommend the latter as it is more cost-effective and does not require a perpetual commitment. For recruitment clusters too isolated for natural dispersal to be effective, not only must birds be translocated to accomplish their initial occupation, but also each time a breeder dies thereafter, another bird must be translocated to the cluster to replace it. It will be difficult and expensive to implement a translocation program as large as this option requires. The recruitment cluster construction required for the other option, in contrast, could readily be accomplished and at only modest expense. If the recruitment cluster construction option is chosen, translocation of selected individuals within the population and enhancing productivity, although probably not essential, may nevertheless be beneficial in further augmenting population growth. Managers may need to undertake a cost-benefit analysis to determine whether to engage in these activities (see below).

Elsewhere it has proven possible to increase populations through natural dispersal to strategically placed recruitment clusters without employing translocation or enhancing productivity. In fact, population growth rates of 1.10 or even higher have been observed, even in small populations (Conner et al. 2001). The most relevant example is the population at Camp Lejeune in North Carolina, which has increased in response to such management from a size similar to SRS in 1991 (27 groups) to 62 groups in 2001, an increase of 130% in 10 years (Walters, unpublished data).

The implications of our results are largely specific to SRS. General results that might be extrapolated to other populations are that small populations can be remarkably stable, and that recruitment clusters that are not in close enough proximity to existing territories are ineffective in promoting population growth. The unfavorable distribution of recruitment cluster locations precluded assessment of the relative effectiveness of different rates of construction or strategies for choosing among locations. Lack of difference between the methods should be considered a result specific to SRS and its existing set of recruitment clusters.

The Role of Enhanced Productivity

Although fledgling dispersal is relatively inefficient, that is, relatively few fledglings actually manage to secure breeding vacancies (Table 3), occupation of existing empty territories and planned recruitment clusters, because of their distances from occupied territories, is highly dependent upon it. This is why enhanced productivity had such a large effect on population behavior in our simulations: increased productivity translated into more dispersing fledglings that might discover isolated vacant territories. Although enhancing productivity was the most effective means of improving population behavior in our simulations, there are two reasons why this may not be a viable management strategy. First, there is some question about the degree to which productivity can be improved through management, if it can be improved at all. Second, the effect of enhanced productivity likely will be diminished as the spatial distribution of recruitment clusters improves.

If recruitment clusters are placed near existing territories, most breeding vacancies will be filled through short-distance dispersal by helpers and fledgling females, and long-distance dispersal by fledgling males and females will become less important. In fact, in populations with

favorable spatial distributions, breeding vacancies are quickly filled through short-distance dispersal processes. In contrast, at SRS breeding vacancies on isolated territories persist, as they are only occasionally filled through long-distance dispersal by fledglings. Enhancing productivity will remain an effective way to improve population behavior only if managers at SRS continue to rely on widely distributed recruitment clusters. We have argued that this is an overly intensive, expensive, and probably ineffective strategy for stimulating population growth.

The level of enhanced productivity used in the simulations (0.7 fledglings per group) exceeds the observed difference between productivity at SRS and the standard reproductive parameters derived from Sandhills data (0.5 fledglings per group, Table 2). The value used represents the estimated effect size when nesting cavities are protected from nest predators and cavity kleptoparasites (Laves and Loeb 1999). Can the level of enhancement used in the simulations be achieved through protection of nest cavities throughout the population? First, it is not clear whether the high levels of productivity observed at SRS are attributable to management or to features of the site (see above). That is, all or most of this enhanced productivity might occur without management of nest predators and cavity kleptoparasites. Second, it is not entirely clear that the increase in productivity observed by Laves and Loeb (1999) in their experimental study was due to their control of nest predators and cavity kleptoparasites. Since these species prevent nesting by occupying cavities and destroy nests, the expected effects were increased frequency of nesting and decreased whole brood loss in treated sites. The difference in productivity between treated and control sites was indeed due to a difference in whole brood loss in one year, but in the second year it was due to a difference in partial brood loss, and no effect on frequency of nesting was observed in either year. Thus the results of the experiment are somewhat difficult to interpret, and results of other similar studies are inconsistent (Conner et al. 1996; Loeb and Hooper 1997; Mitchell et al. 1999). The most reasonable conclusion based on the available data is that some species of nest predators and cavity kleptoparasites affect productivity in some populations of red-cockaded woodpeckers in some years (Conner et al. 2001). Certainly whether one can reliably increase productivity by protecting nest cavities is questionable. We conclude that making enhancement of productivity a key element of a strategy to promote population growth is not advisable. That said, it may nevertheless be worthwhile to make a limited investment in enhancing productivity, at least as long as the population remains small (i.e., < 50 groups) and some isolated recruitment clusters are present (see below).

Model Performance

In most cases, the simulated population did not perform as well as the actual population. The most obvious explanation of this is that model results are biased because the model is parameterized using data from a population other than SRS (i.e., North Carolina Sandhills). Specifically productivity and survival values at SRS (Tables 1 and 2) are higher than those used in the model. Thus it is encouraging that the enhanced productivity simulation matches observed population behavior so well, as this scenario uses parameter values that come closest to those characteristic of SRS during the study period. Although adult survival is still underestimated in this scenario, productivity is overestimated, resulting in a fairly close match to SRS demography overall. Site-specific parameters for SRS are based on a rather small sample, in terms of both numbers of birds and numbers of years, so it would not necessarily be better to use these values rather than the standard ones in simulations. Annual variation in demography exists, and the high productivity and survival values observed at SRS may represent a series of unusually favorable years rather than a true long-term average. Biases in dispersal parameters might also

affect population performance. We think it unlikely that we have underestimated dispersal abilities of SRS birds, however, because the empirical data we report indicate that dispersal success is poor (Table 3).

Management activities may be another source of discrepancies between observed and simulated population behavior. Activities that were not included in the simulations may further augment population growth in the real population compared to the simulated populations, especially translocation. Through the translocation program at SRS birds have been imported from other populations and, more importantly, located on empty territories. Translocation is designed to improve the efficiency of dispersal to recruitment clusters. It stands to reason that a management activity designed to solve what we have identified as the most important problem in this population will improve population performance. This would be expected to especially affect occupancy of isolated recruitment clusters.

MANAGEMENT IMPLICATIONS

The new SRS Management Plan (Edwards et al. 1998) contains all the elements required of a management strategy that has potential to promote population growth (Walters 1991). It describes for example how the landscape will be managed to provide foraging habitat, how hardwood midstory will be controlled, and how tools such as recruitment stands and artificial cavities will be used. In essence, it is a broad outline of how the woodpeckers will be managed. The population objectives set forth in the Management Plan are to increase the population to 30 groups by the year 2000, a goal that has been achieved, and to 429 groups ultimately (Edwards et al. 1998). Details of implementation have the potential to determine whether or not a sound management plan is successful. The challenge at SRS currently is to identify an implementation strategy that will stimulate continued growth toward the ultimate population objective at a reasonable rate, and at a reasonable cost.

We recommend continuing construction of recruitment clusters, but altering the strategy for their placement to locate them within dispersal range of helpers on several territories. This seems to us the best means to increase the contribution of natural behavior to population growth, and reduce the required contribution of intensive and expensive management. We advocate using 2 km as the critical distance, based on Chadwick's (2001) results. This distance falls within our best estimate of the dispersal range of helpers, 3 km (Daniels 1997, Figure 4.2), which is the value we use in the model (Letcher et al. 1998). If this strategy is sound, the rate of transition from helper male to breeder (and perhaps fledgling female to breeder) should increase once the new strategy for locating recruitment clusters is employed. If this proves true, population growth will become less dependent on fledgling dispersal, especially fledgling male dispersal, and translocation and enhancement of productivity will become less effective, and less necessary, in stimulating population growth. However, these management activities are likely to retain some degree of effectiveness, especially in the transition period before recruitment clusters close to active territories become widely available. Continuing these activities, but at a less intensive, and therefore less expensive, level may be prudent. We recommend continuing translocation, but limiting it to intrapopulation movements, specifically translocation of young females to unpaired males and of young males to recruitment clusters that fail to become occupied within a reasonable time (i.e., 2-3 years). Similarly, we recommend continuing to enhance productivity, but limiting this to passive rather than active means, specifically employing SQEDs rather than actively removing flying squirrels from woodpecker cavities. Adaptive management should continue, that is, the effectiveness of each technique should be

monitored as better-placed recruitment clusters become more readily available and the population grows.

CONCLUSION

The red-cockaded woodpecker population at the Savannah River Site, as currently configured, appears reasonably stable considering its size. Current management is achieving modest growth rates through a combination of natural population dynamics and intensive management of individual birds and clusters. Low rates of transition from nonbreeder to breeder status are limiting contributions of natural population dynamics currently, and this is attributable to low efficiency of nonbreeders in locating recruitment clusters. The results of this study suggest that this problem can be overcome by placing recruitment clusters in closer proximity to more active territories. By this means, higher growth rates can be achieved while reducing intensity of management.

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