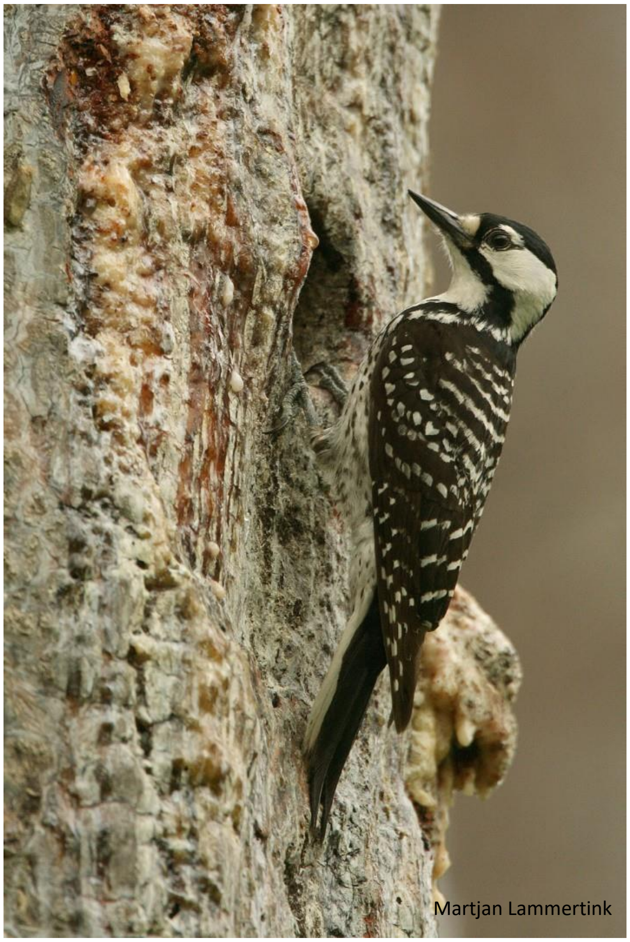
Species Status Assessment Report For
the
Red-cockaded Woodpecker (*Picoides borealis*)
Version 1.3



April 2020
U.S. Fish and Wildlife Service
Atlanta, GA

ACKNOWLEDGEMENTS

This document was prepared by the red-cockaded woodpecker species status assessment (SSA) core team: Stephanie DeMay (Virginia Tech), Jeff Walters (Virginia Tech), Mike Marshall (FWS-Texas A&M), Will McDearman (FWS), John Hammond (FWS), Debby Crouse (FWS), Angela Romito (FWS), and Matthew Dekar (FWS). Additional input on scientific and technical assessment methods was provided by SSA expert team members: Robin Boughton (FL Fish and Wildlife Conservation Commission), Reed Bowman (Archbold Biological Station), Jonathan Burnam (GA Department of Natural Resources), Larry Carlile (Fort Stewart), Jay Carter (Jay Carter and Associates), Ralph Costa (RCWO), John Carpenter (NC Wildlife Resources Commission), Caroline Causey (SC Department of Natural Resources), Kathy Gault (Eglin Air Force Base), Susan Haig (U.S. Geological Survey Forest and Rangeland Ecosystem Science Center), Bill Holimon (AR Natural Heritage Commission), Nancy Jordan (FWS Carolina Sandhills NWR), Dylan Kesler (The Institute for Bird Populations), Dennis Krusac (U.S. Forest Service), Carl Petrick (U.S. Forest Service), Craig Rudolph (U.S. Forest Service), Craig Tenbrink (Marine Corps Base Camp Lejeune), and Bently Wigley (National Council for Air and Stream Improvement). Peer reviews of a draft of this report were provided by Dr. Daniel Saenz (U.S. Forest Service Southern Research Station), Dr. John Kappes, Jr. (Brosnan Forest), and Dr. Todd Engstrom (Tall Timbers Research Station). Certain sections of Chapter 2, Species Biology, were liberally used or copied from the U.S. Fish and Wildlife Service's 2003 Red-cockaded Woodpecker Recovery Plan. Funding from the Department of Defense supported Stephanie DeMay in a postdoctoral position at Virginia Tech for the SSA. Texas A&M Institute of Renewable Natural Resources funds supported Michael Marshall while on an Intergovernmental Personnel Assignment with the Service.

Suggested reference:

U.S. Fish and Wildlife Service. 2019. Species status assessment report for the red-cockaded woodpecker (*Picoides borealis*). Version 1.3, April 2020. Atlanta, GA.

Table of Contents

Appendix 1: Missing Data Imputation for Ecological Data: A Comparison of Methods Applied to Red-cockaded Woodpecker Viability Analysis

Appendix 2: Future Conditions Model Assessment Methods

Appendix 3: Future Population Simulation Output with Population Size, Time Series Graphs, and Selected Future Parameters for Each Population

Appendix 4: Selected Future Population Model Simulation Output Parameters Under the Manager's, Low, Medium, and High Management Scenarios

Appendix 5: Summary Attributes for Initial and Future Simulated Populations Under the Manager's Expectation, Low, Medium, and High Management Scenarios

Appendix 6: Future Simulated Population Resilience Comparison by Manager's, Low Medium, and High Management Scenarios, with Median Population Size at 25 years and λ

Appendix 7: AIC Model Results from Past Time Series Models and Management Covariates for Small, Medium, and Large Populations

EXECUTIVE SUMMARY

This Species Status Assessment (SSA) report is an analysis of the past, current, and estimated future condition of the red-cockaded woodpecker (*Picoides borealis* = *Dryobates borealis*). The assessment was conducted in the SSA framework of the U. S. Fish and Wildlife Service (Service) for species viability in terms of resilience, redundancy, and representation. Resilience is the ability of a population to withstand stochastic disturbance events. Redundancy is the ability of a species to tolerate stochastic and catastrophic events by virtue of multiple resilient populations. Representation is the capacity of a species to adaptively respond to environmental change.

The red-cockaded woodpecker (RCW) is a non-migratory territorial resident of fire-dependent, open, mature and old southern pine forests, particularly in the longleaf pine ecosystem. RCWs are cooperative breeders. A breeding group consists of the breeding male and female with 0 – 6 non-breeding adult helpers. Each RCW occupies its own cavity excavated into the heartwood of living pines that are at least 65-80 years old, and typically much older. Each group defends its territory of cavity trees and foraging habitat from other groups. A single group territory and home range where birds forage for invertebrates on and under the bark of larger and older living pines may be upwards to 162 hectares (400 acres), though much less depending on habitat quality and neighboring group density,

The pre-settlement landscape of open longleaf and other pine forests probably covered more than 247 million acres potentially supporting 1.5 million or more RCW potential breeding groups. The loss of widespread suitable forest conditions has been well documented in response to extensive cutting throughout the early 1900s, followed by conversion to agriculture and other non-forest uses, and fire suppression with subsequent intensive forest management practices favoring incompatible short-rotation even-aged silviculture in remaining forests. The RCW was one of the first species listed as endangered in 1973 under the Endangered Species Act of 1973.

By 1973 or shortly afterwards, the best available rangewide estimates were about 10,000 individual RCWs in no more than 4,000 groups. The species continued to decline after listing as indicated by repeated surveys of the number of active clusters, mostly on public lands. A decline of at least 23% since 1980 was estimated from repeated surveys of those sites by 1990. However, the 1990s were a significant decade for RCW conservation and recovery with new science, management, and understanding of population dynamics and limiting factors. Cavity limitations due to insufficient old pines for natural cavities could be alleviated by the advent and installation of artificial cavities in younger pines to sustain existing active clusters with breeding groups. Moreover, populations could be increased by inducing new group formation at recruitment clusters with artificial cavities in restored habitat suitable for foraging. These and other elements became an integrated recovery strategy by the late 1990's, incorporated in the Service's 2003 recovery plan, and implemented by various federal, state and other landowners that halted and began to reverse the historical decline. Successful management to stabilize and increase populations also further demonstrated that the RCW is a conservation-reliant species. It depends on active management including the provision of artificial cavities until forest conditions support adequate old pines for natural cavity excavation, prescribed fire and compatible forest management to restore and maintain suitable habitat for cavity trees and foraging, establishment of recruitment clusters to increase population size, translocation to augment growth of vulnerable small populations and for reintroduction, and effective monitoring to affirm the response to management.

Current Conditions

We categorized resilience for 124 demographic populations across the range of the RCW based on population size, and used population growth rate as a secondary factor to indicate relative resilience of populations within each of five resilience categories. We defined a demographic population as the spatial aggregation of active clusters/territories where a breeding vacancy is likely to be replaced by a RCW from within the population. We used RCW dispersal data from long-term monitoring data and radio-telemetry studies to spatially delimit demographic populations according to nearest-neighbor active clusters within 6 km (3.7 miles). This was the approximate 95th percentile of the distance juvenile females foray from their natal territory to search for a breeding vacancy in another territory. We acquired current and recent GIS data for the longest available past time-series mostly from federal and state agencies to delineate demographic populations. Demographic population size by year was based on either the number of active clusters by GIS or data from the Service's Annual RCW Property Report database when a database report corresponded to a single demographic population. Population resilience categories were very low (<30 active clusters); low (30-99 active clusters); moderate (100-249 active clusters); high (250-499 active clusters); and very high (>500 active clusters). We selected these categories based on previous RCW individual-based spatially explicit modeling studies that identified population size thresholds that affected vulnerability to stochastic demographic and environmental events. To calculate growth rates for a current demographic population, we used past time series abundance data (active clusters) from as many years as possible from 1998 to 2017. When we had at least five years of past abundance data we estimated a constant population growth rate according to the initial and final population size to produce the observed change in population size. Based on these rates we categorized populations as decreasing ($\lambda < 1$), increasing ($\lambda > 1.02$) or stable ($\lambda = 1.00\text{-}1.02$).

Of the 124 populations analyzed, we classified the current resilience of three populations as very high, three as high, 10 as moderate, 37 as low, and 71 as very low. Thirteen populations have decreasing growth rates, 66 are increasing, 19 are stable, and rates for 26 could not be assessed because of inadequate data. All assessed populations in the very high, high and moderate resilience classes currently have stable or increasing growth rates. The 13 populations with decreasing growth are restricted to the low and very low resilience classes. Stable and increasing growth rates of 73 populations in the inherently low and very low resilience categories reflect positive effects of management for this conservation-reliant species.

We assessed representation primarily on life history variation and ecological and geographic diversity among 13 ecoregions, 11 of which represented recovery units in the 2003 RCW recovery plan. We report redundancy in terms of the number of populations by resilience classes, and representation as a matrix of the number, redundancy, and distribution of populations by resilience class among ecoregions. Representation has decreased significantly relative to the historical distribution and abundance of the species. However, representation in terms of species presence and absence in ecoregions has not decreased further since the 2003 recovery plan was developed and subsequently implemented.

Of 124 current demographically delineated populations, redundancy of very high (3) and high (3) resilience populations is low. Redundancy of very highly to moderately resilient populations also is low within and among ecoregions. The total number of populations gives the appearance of greater redundancy, but this redundancy is manifested in populations of low or very low resilience. Of the 13 ecoregions with current populations, those with high (3) or very high (3) resilient populations are restricted to only four regions: Mid-Atlantic Coastal Plain, East Gulf Coastal Plain, South Atlantic Coastal Plain, and Sandhills. Only two ecoregions, the East Gulf Coastal Plain and the Sandhills, have more than one population classified as of high or very high resilience, and only these two regions have more than two populations classified as moderately to very high resilience. Only four ecoregions (South Atlantic Coastal Plain, Mid-Atlantic Coastal Plain, West Gulf Coastal Plain, Upper East Gulf Coastal Plain) have two populations of moderate to high resilience, and thus some level of redundancy in terms of relatively resilient populations. All of the populations in six ecoregions are of low or very low resilience, but are important for representation in their respective regions and across the range.

RCW populations and habitat are periodically subjected to disturbances including those from ice storms, tornados, and hurricanes that increase mortality, destroy cavity trees and foraging habitat, and cause population declines. Populations in the West Gulf Coastal Plain (17), East Gulf Coastal Plain (14), Florida Peninsula (22), South Atlantic Coastal Plain (10), and Mid-Atlantic Coastal Plain (24) are particularly vulnerable to periodic hurricanes. Of these 124 populations, most (87) reside in coastal plain ecoregions including the six populations with very high and high resilience. Four populations of moderate resilience and one population of very high resilience occur further inland in three interior ecoregions. Since 1998, every population in coastal plain ecoregions has been affected by one or more hurricanes, although without extirpation. Post-storm management has been critical to mitigate impacts by the installation of artificial cavities, reducing hazardous fire fuels from woody debris, and restoring suitable forest composition and structure.

Future Conditions

Most of the 124 current demographic populations have benefitted from various conservation management actions to sustain or increase populations over the past 20 years. Past population performance may be indicative of future population performance to the extent management that sustained and increased populations in the past continues in the future. To determine population viability and its dependence on management, we assessed the future condition for RCW populations by modeling past trends in population growth and size as a function of environmental and management covariates. Populations were separately modeled as small (6 – 29), medium (30-75), and large (>75) active cluster classes, and we combined all populations with each size class to create global size class models of RCW population growth. For past growth rate of small populations, the best model included effects of number of new recruitment clusters (recruitment clusters), number of new artificial cavities in previously existing clusters (cavity management), midstory treatments by prescribed fire or mechanical methods (midstory any method), number of RCWs translocated into the population, and dominant pine type. Translocation had the greatest management effect on growth. For medium populations, recruitment clusters and midstory treatments by prescribed fire were significant management covariates. The best model for large populations included recruitment clusters, cavity management, and spatial configuration of active clusters. In all cases, effects of recruitment clusters, cavity management and midstory treatment were positive. Greater spatial aggregation of clusters promoted population growth in large populations.

To assess future resilience of populations, we used best fit linear models of past population growth for small, medium, and large populations to stochastically simulate the dynamics of current demographic populations for 25 years by 1-year increments beginning with their initial current population size. Populations with less than six active clusters were not simulated. We then categorized the resilience of future populations according to their projected size and growth rate in the same manner as with current population resilience. This was done for four management scenarios, Manager's Expectation (84 populations), Low Management (81), Medium Management (84), and High Management (81). The number of demographic populations at the end of the 25-year simulation period varied among scenarios depending on the number of initially separate populations that demographically merged following growth to form a larger single demographic population. We simulated each population with 5,000 replicate runs during the 25-year period. When a population increased or decreased during a simulation from one size-class and model to another, the population size-class model changed accordingly.

Future values for significant habitat and management model covariates for the Manager's scenario were obtained by our elicitations to property biologists, foresters, and managers who assumed the RCW remains a federally listed species for the future 25-year period. For the Low scenario, values for each management covariate were set to zero. The Low scenario estimates the impact of eliminating vital single species management techniques designed specifically for

RCWs, and thus relying on ecosystem management alone. The Medium scenario represents population projections based on the assumption that the management employed over the past 20 years will continue for the next 25 years. Values of Medium Management scenario covariates were selected as the overall median from all past population data. The High scenario represents projections of what might potentially be achieved should the species be systematically managed more intensively across its range than it has been in the past. Values of management covariates in the High scenario were selected from the approximate 90th percentile of all combined populations in the past model. In all scenarios, future population size was limited by carrying capacity. We obtained carrying capacity estimates for each population from property and population managers.

Five populations have very high resilience under all management scenarios at year 25 (Apalachicola National Forest-St. Marks NW-Tate's Hell State Forest, North Carolina Sandhills, Fort Stewart, Eglin Air Force Base, and Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA). Only one other population has sufficient carrying capacity to attain very high resilience (Bienville National Forest X), but it did not increase to this level even under High Management. Results of the Manager's Expectation and Medium Management scenarios were similar, suggesting that managers expect to manage with moderate intensity in the future. The seven populations in the high resilience class were the same in the Manager's and Medium scenarios. However, the Medium scenario projected fewer populations with negative growth rates and slightly better improvements in resiliency compared to the Manager's scenario.

The Low and High Management scenarios projected more extreme future resilience conditions. Results of these simulations, and their contrast to those for the Manager's and Medium scenarios, illustrate the extent to which the RCW is a conservation-reliant species that depends on appropriate management to sustain its populations. They also show how appropriate management can sustain even small populations with low or very low resilience. Low Management projects only a modest increase over current conditions in the proportion of populations that will have moderate, high or very high resilience, and a dramatic deterioration of small populations that currently have low or very low resilience. The High Management scenario, with nine highly resilient and five very highly resilient populations, is a close approximation to the maximum resiliency achievable for RCWs given the current land base for conservation and their 25-year carrying capacities, as nearly all populations reach this limit in this scenario. This suggests that habitat availability rather than potential for population growth limits the future numbers of RCWs. Populations in the very low resilience class currently are the most vulnerable to extirpation, but management simulated in the High scenario sustains and in a few cases increases these populations.

Most small populations are projected to be in serious risk of extirpation in the Low Management scenario. Fifty-eight populations are projected to have negative population growth rates, compared to 11, 2 and 0 in the Manager's, Medium and High management scenarios respectively. Most populations projected to have negative growth rates are in the very low (< 30 active clusters) resilience category (48/58 Low, 10/11 Manager's, 2/2 Medium). Also, 10 of 12 populations in the low resiliency category are projected to have negative growth rates under Low Management, compared to only one in all the other scenarios combined.

Patterns of representation are most similar for the Manager's and Medium scenarios due to the 12 populations in common among the very high and high resilience classes distributed among six ecoregions. The greatest population redundancy for these resilience classes is within the East Gulf Coastal Plain with two high and two very high resilient populations. Each of five other ecoregions have at least one population with either a high or very high resilience class. Seven ecoregions lack any populations with high or very high resilience. Representation and redundancy is greatest in the High scenario with 14 high and very high resilient populations distributed among seven of the 13 ecoregions. Conversely, representation and redundancy is most diminished in the Low scenario with 10 high and very high populations among five ecoregions.

Compared to current conditions, there is potential to make significant gains in representation and redundancy over the next 25 years, but only with future management represented by the Manager's, Medium, and High scenarios. A greater number of high and very high resilience populations are projected to be more widely distributed among ecoregions and to include the western geographic range under Medium and High management in the future. Over the wide geographic range of this species, the occurrence of high and very high resilience populations is most concentrated in the East Gulf Coastal Plain and Sandhills.

Many decades are required to attain a desired future ecosystem condition in which RCWs are no longer dependent on artificial cavities and related special treatments. Without adequate species-level management, in contrast to ecosystem management alone, very little increase in the number of moderately to very highly resilient populations can be expected, and small populations of low or very low resilience are unlikely to persist. Our Low Management scenario represents this condition. It does not represent the absence of any RCW management, as all populations in the past model are actively managed to some degree (e.g., artificial cavities and forest management to provide nesting and foraging habitat), and thus some baseline level of management occurs in all models, even in the Low Management scenario. Our models therefore cannot estimate the cumulative effects of fire suppression and forest practices that led to the decline of the RCW and caused it to become endangered. Adverse impacts of these practices is well documented, and it is clear that a return to them would lead to extirpation of populations and the species. Effective ecosystem management will be necessary in perpetuity if the RCW is to persist, and in the foreseeable future single-species management will be necessary as well to prevent populations from being lost.

Carrying capacity may be underestimated in our analyses. Recently there have been numerous anecdotal reports and one excellent study of pockets of very high densities of RCWs in prime habitat within several populations. If carrying capacity estimates are overly conservative, and the high densities of RCWs that occur in high quality habitat suggest they are, then greater growth than our simulations project and larger differences between management scenarios are possible.

Our future simulations do not adequately represent potential impacts of hurricanes. The past population models as used to parameterize future models included past hurricanes to the extent particular populations were affected and caused annual variation in growth rates. However, these past trends do not necessarily predict the future location or intensity of hurricanes during a future 25-year period.

CHAPTER 1: INTRODUCTION

The red-cockaded woodpecker (RCW, *Picoides borealis=Dryobates borealis*) is a territorial, non-migratory bird species that makes its home in mature pine forests in southeastern United States. The RCW was listed as endangered in 1970 (35 Federal Register 16047) under the Endangered Species Conservation Act of 1969, and carried forward under the subsequent Endangered Species Act in 1973. Once a common bird distributed continuously across the southeastern United States, by the time of listing the species had declined to fewer than 10,000 individuals in widely scattered, isolated, and declining populations (Jackson 1971, Ligon et al. 1986).

In 1993, the RCW consisted of about 4,694 rangewide active clusters or active territories. Today, the U.S. Fish and Wildlife Service (Service) conservative rangewide estimate is about 7,800 active clusters. Of 20 RCW populations required for downlisting according to the 2003 RCW Recovery Plan, 13 have attained downlisting population size objectives. Population growth rate estimates for 6 of the 7 remaining populations indicate these populations should attain downlisting population size objectives in the next 10-15 years. The status and recovery objectives of the Northeast North Carolina/Southeast Virginia Essential Support recovery population, which has not attained its downlisting recovery population size objective, are under Service review to assess the occurrence of other RCWs in this landscape and management limitations in pocosin and other unusual habitat types. Elsewhere on other public land, about 332 RCW clusters occur on properties not associated with designated recovery populations. In addition, other RCWs include 835 active clusters enrolled in the Safe Harbor Program for 420 mostly private landowners across nine states.

The improving status of this species and the recent advent of the Service's Species Status Assessment (SSA) Framework led the Service to initiate this RCW SSA. The SSA framework (USFWS 2016) is intended to support an in-depth review of the species' biology and threats, an evaluation of its biological status, and an assessment of the resources and conditions needed to maintain long-term viability. The intent is for the SSA to be easily updated as new information becomes available and to support all functions of the Endangered Species Program.

Using the SSA framework (Figure 1), we consider what the species needs to maintain viability by characterizing the status of the species in terms of its resiliency, redundancy, and representation (Wolf et al. 2015).

- **Resiliency** describes the ability of populations to withstand stochastic events (arising from random factors). Resilience is related to population size, growth rates, and the response to stochastic events. Highly resilient populations are better able to withstand disturbances such as random fluctuations in birth and mortality rates (demographic stochasticity), variation in meteorological and other environmental conditions (environmental stochasticity), or the effects of anthropogenic activities.

- **Representation** is the ability of a species to adapt to changing environmental conditions. Representation can be measured by the breadth of genetic, environmental, or life history diversity within and among populations and gauges the probability that a species is capable of adapting to environmental changes. The more representation, or diversity, a species retains, the more it is capable of adapting to natural or human caused changes in its environment. In the absence of species-specific genetic and ecological diversity information, we evaluate representation based on the extent and variability of habitat characteristics across the geographical range.
- **Redundancy** describes the ability of a species to withstand catastrophic events. Measured by the number of populations, their resiliency, and their distribution and connectivity, redundancy gauges the probability that the species can withstand or recover from catastrophic natural or manmade events.

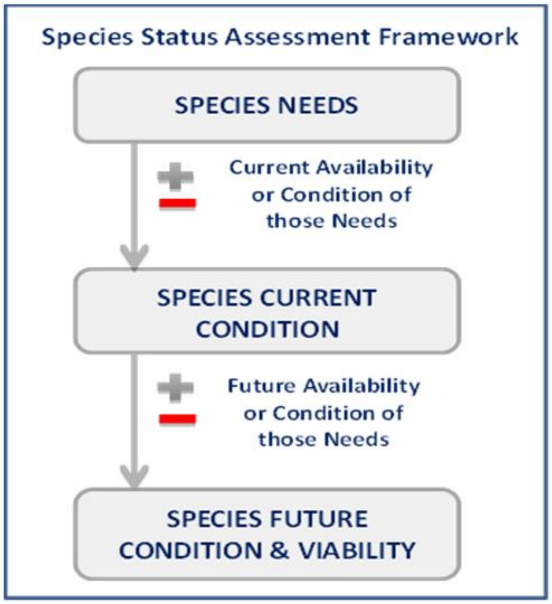


Figure 1- Species Status Assessment Framework

To evaluate the biological status of the RCW both currently and into the future, we assessed a range of conditions to consider the species' resiliency, redundancy, and representation (together, the 3Rs). This report provides an assessment of biology and natural history and assesses demographic risks, stressors, and limiting factors in the context of determining the viability and risks of extinction for the species. The format for this SSA includes: (1) the species biology and life history (Chapter 2); (2) the species needs and approaches to assessing resilience, redundancy and representation (Chapter 3); (3) current condition of the species (Chapter 4) (4) influences on species' viability including risk factors (Chapter 5); and (4) future condition of the species (Chapter 6). This document is a compilation of the best available scientific and commercial information and a description of past, present, and likely future viability and risk factors to the RCW.

CHAPTER 2: SPECIES BIOLOGY

In this chapter, we provide basic biological information about the RCW, including its taxonomic history, species description, distribution, life history, ecology, and habitat characteristics. We then use this information to outline the resource needs of RCWs.

Taxonomy

The RCW is a long and well established taxonomic species, although with some nomenclatural changes for its proper genus. Jackson (1971) provided a detailed review of the early history of RCW taxonomy and nomenclature. RCWs were first described as *Picus borealis*, "le pic boreal", by the French businessman and amateur naturalist Vieillot (1807). The RCW was classified as *Dryobates borealis* in American Ornithological Union (AOU) 1st 1886 checklist of North American birds, that was later changed in the AOU 1946 22nd supplement to the 4th AOU checklist edition to *Dendrocopos borealis borealis* (AOU 1947), followed by *Picoides borealis* in the AOU 6th 1983 edition (AOU 1982).

Just recently in the American Ornithological Society's (AOS) 18th supplement to the 7th edition of the *Check-list of North American Birds* (Chesser et al. 2018), the classification as *Picoides borealis* has been changed and returned to *Dryobates borealis*. The AOS is the descendant organization formed by a merger of the American Ornithologists' Union and Cooper Ornithological Society. The AOS Committee on Classification and Nomenclature (Chesser et al. 2018) considered, among other data, results of phylogenetic analyses with nuclear and mitochondrial DNA (Weibel and Moore 2002a, 2002b, Winkler et al. 2014, Fuchs and Pons 2015, Shakya et al. 2017) that the genus *Picoides* was not monophyletic. As a result, the genus *Picoides* was retained for the three-toed woodpeckers (American three-toed woodpecker – *P. dorsalis* and the black-backed woodpecker-*P. arcticus*) and all other North American woodpeckers formerly as *Picoides* were transferred to *Dryobates*.

Fuchs and Pons (2015), based on their phylogenetic analysis of the pied woodpecker assemblage and related studies, proposed *Leuconotopicus* as a monophyletic group with *borealis* and four other species. Although the AOS does not accept *Leuconotopicus*, the RCW is classified as *L. borealis* by the International Ornithological Congress (IOC) World Bird List (v8.2) (Gill and Donsker 2018), while still treated as *Picoides borealis* in the most recent "Clements" list of birds of the world (Clements et al. 2017).

The AOS taxonomy and nomenclature for species in the *Checklist of North and Middle American Birds* is accepted by most of the scientific community in the United States, at least in part due to the process for classification analysis by the Committee on Classification and Nomenclature. In this document for and by the Service, our use of *Picoides borealis* reflects the fact that this is the federally listed endangered taxon. Any change by the Service to another genus in the taxonomic classification for the listed RCW must be in accord with the Code of Federal Regulations (50 CFR 17.11) implementing the Endangered Species Act to amend the list of endangered and threatened wildlife. The different classifications of the proper genus for the RCW do not reflect any taxonomic dispute on the biological validity of this species. The different RCW genera have reflected different classification systems and associated nomenclatural requirements for groups of woodpecker species.

In 1941, Wetmore (1941) proposed a new RCW subspecies, *Dryobates borealis hylonomus* for birds with shorter wings in central and southern peninsular Florida. This subspecies was adopted in the AOU 1946 22nd supplement to the 4th AOU checklist edition (AOU 1947) with the nominal *Dryobates borealis borealis.* However, Mengel and Jackson (1977) studied a larger series of rangewide specimens and found variation in culmen length, wing length and tail length in the species to be smoothly clinal, concluding there was no justification for geographically distinguishing birds in south Florida or elsewhere as a subspecies. The AOU removed *D. b. hylonomus* as a subspecies in the 6th 1983 edition (AOU 1982), reverting to the single species *Picoides borealis*. Dryobates borealis hylonomus (Wetmore) also was not included as a subspecies in the IOC World Bird List (v8.2) (Gill and Donsker 2018) or Clements world list (Clements et al. 2017). As listed by the Service, *D. b. hylonomus* also is not recognized as a subspecies.

Species Description

Wilson gave the species the English common name we use today, red-cockaded woodpecker, in reference to the several red feathers of males, located between the black crown and white cheek patch, which are briefly displayed when the male is excited. In Wilson's time, "cockade" was a common term for a ribbon or other ornament worn on a hat as a badge. The cockade is a poor field mark because it is rarely seen in the field, but it does identify the sexes of adult birds in the hand.

RCWs are relatively small. Adults measure 20 to 23 cm (8 to 9 in) and weigh roughly 40 to 55 g (1.5 to 1.75 oz; Jackson 1994, Conner et al. 2001a). RCWs are larger than downy woodpeckers (*Picoides pubescens*), similar in size to yellow-bellied sapsuckers (*Sphyrapicus varius*), and smaller than other southeastern woodpeckers. RCW size varies geographically and clinally, with larger birds generally to the north (Mengel and Jackson 1977).

RCWs are black and white with a ladder back and large white cheek patches (Figure 2). These cheek patches distinguish RCWs from all other woodpeckers in their range. RCWs are black above with black and white barring on their backs and wings. Their breasts and bellies are white to grayish white with distinctive black spots along the sides of the breast changing to bars on the flanks. Central tail feathers are black and outer tail feathers are white with black barring. Adults have black crowns, a narrow white line above the black eye, a heavy black stripe separating the white cheek from a white throat, and white to grayish or buffy nasal tufts. Bills are black, and legs are gray to black.

Figure 2. Adult female (left) and male (right) RCW.

Excepting the red cockade, RCWs are monomorphic and the sexes are generally indistinguishable in the field. The small cockade is not normally visible beneath crown feathers. In contrast, sexes of juveniles can be distinguished in the field until the first fall molt, because juvenile females have all black crowns whereas juvenile males have red crown patches. Nestlings can be sexed in the hand, in some cases as early as eight days of age: capital feather tracks, observed through the transparent skin before feather emergence, appear grayish black in females and reddish in males (Jackson 1982).

Juveniles may be distinguished from adults in the field by duller plumage, the presence of white flecks just above the bill on the forehead, and diffuse black shading in the white cheek patch. In the hand, RCWs can be aged by the relative length and shape of the vestigial tenth primary until this primary is molted in the fall. This primary is longer and more rounded in juveniles than in adults (Jackson 1979). Second-year birds are distinguishable from older birds: because juveniles do not molt their secondaries during their first fall molt, the secondaries of second-year birds appear more worn and brown in contrast to newer black primaries (Jackson 1994).

Distribution

RCWs once were common throughout the longleaf pine ecosystem, which covered at least 90 million acres before European settlement (Frost 2006). Historical population estimates are 1-1.6 million family groups (Conner et al. 2001a), the social unit of RCWs. The birds inhabited the open pine forests of the southeast from New Jersey, Maryland and Virginia to Florida, west to Texas and north to portions of Oklahoma, Missouri, Tennessee and Kentucky.

The longleaf pine ecosystem was eliminated from much of its original range because of early (1700s) European settlement, followed by the naval stores/turpentine industry (1800s) and widespread commercial timber harvesting. Early to mid-1900 commercial tree farming, urbanization and agriculture contributed to further declines. Much of the remaining habitat is very different from the vast, historical pine forests in which RCWs evolved. The second growth longleaf pine forests of today, rather than being dominated by centuries-old trees as the original forests, are just reaching that age (90-100 years) required to meet all the needs of the RCW. Furthermore, in many cases the absence of fire has caused the original open savannahs to degrade into dense pine/hardwood forests.

More detail will be given in the SPECIES NEEDS section (historical and current distribution).

Life History

Cooperative Breeding

RCWs live in groups that share, and jointly defend, all-purpose territories throughout the year. Group living is a characteristic of their cooperative breeding system. RCWs are one of only a handful of bird species found in the United States that exhibit this unusual social system. In cooperative breeding systems, some mature adults forego reproduction and instead assist in raising the offspring of others (Emlen 1991). The cooperative breeding system of RCWs is well studied, and several reviews are available (Walters 1990, Jackson 1994, Walters and Garcia 2016). In this species, most helpers are males that remain and assist the breeders, who typically are their parents or other close kin, on their natal territory (Ligon 1970, Lennartz and Harlow 1979, Lennartz et al. 1987, Walters et al. 1988a). Some females become helpers on their natal territories as well, and a few individuals of each sex disperse to become helpers of unrelated breeders in other groups (Lennartz et al. 1987, Walters et al. 1988a, Walters and Garcia 2016). Helpers are strictly non-breeders (Haig et al. 1994b), but participate in incubation, feeding and brooding of nestlings and feeding of fledglings, as well as territory defense, nest defense, and cavity excavation. Groups may contain as many as 5 helpers, but most groups consist of only a breeding pair with no helpers, or a breeding pair plus 1-2 helpers. Groups containing more than 2 helpers are uncommon, but are increasing in frequency as habitat improves (Walters and Garcia 2016).

RCW groups are highly cohesive. Each individual has its own roost cavity, but typically group members congregate immediately after emerging from their cavities at dawn, and then move together through their large territories until they return to their cavities at dusk. Much like a primate troop, they visit only a portion of their territory or home range each day, and travel different routes on different days.

Group formation is best understood in terms of alternative life-history tactics practiced by young birds (Walters 1991, Walters and Garcia 2016). Young birds may either disperse in their first year, or they may remain on the natal territory and become a helper. The proportion of each sex adopting each strategy varies among populations (Lennartz et al. 1987, Walters et al. 1988a, DeLotelle and Epting 1992, Walters and Garcia 2016), but first-year dispersal is the dominant strategy for females whereas both strategies are common among males. A dispersing individual, if it survives, may become a breeder at age one, but many fail to locate a breeding vacancy and exist as a floater at age one, or in a few cases as a helper in a new group (Walters et al. 1988a, 1992a, Walters and Garcia 2016). Some dispersing males locate a territory but no mate, and hence are solitary males at age one. Solitary males and floaters, like helpers (see below), may become breeders at subsequent breeding seasons.

It is those individuals who choose to remain on their natal territory as helpers rather than disperse that are primarily responsible for group formation. Individuals may remain helpers up to age 11, but most become breeders within a few years (Walters et al. 1988a, 1992a). Male helpers may become breeders by inheriting breeding status on their natal territory or by dispersing to a nearby territory to fill a breeding vacancy. When helpers move, it is usually to an adjacent territory, and they rarely disperse across more than 2 territories (Kesler et al. 2010). Female helpers almost never inherit the breeding position on their natal territory, instead relying on dispersal to neighboring territories to become breeders. Females rarely remain on their natal territory as helpers beyond age 3 (Walters and Garcia 2016). Birds of both sexes that disperse to become unrelated helpers often inherit breeding status in their new group.

In contrast to the short-distance dispersal of helpers, individuals of both sexes dispersing in their first year sometimes move long distances, more than 100 km (62 miles) in a few cases (Walters et al. 1988b, Conner et al. 1997c, Ferral et al. 1997). However, typical dispersal distances of juveniles are much lower than in other avian species. The median dispersal distance of juvenile females is only 2 territories from the natal site, and about 90% settle 1 to 4 territories from the natal site (Daniels 1997, Daniels and Walters 2000a, Kesler et al. 2010). Males are even more sedentary, since many of them adopt the helping strategy. About 70% of males become breeders on the natal territory or an immediately adjacent one (Daniels 1997, Kesler et al. 2010). The seeming paradox between generally short dispersal distances and numerous records of very long movements arises from the occurrence of 2 dispersal modes among juveniles. Juveniles, many of which overwinter on the natal territory, engage in forays, visiting other territories up to 6-8 km (3.7 – 5.0 miles) from the natal territory, and then disperse within that range. However, some, after a period of foraying, abruptly depart the area and move far beyond their previous foraying range, moving 20 km (12.4 miles) or more in a single day. These "jumpers" account for the observed long distance movements of juvenile RCWs (Kesler et al. 2010).

Once a male acquires a breeding position, by whatever pathway, he almost invariably holds it until his death (Walters et al. 1988a). Females, however, regularly practice breeding dispersal: approximately 10% of breeding females switch groups between breeding seasons each year (Walters et al. 1988a, Daniels and Walters 2000b). Females invariably depart when their sons inherit breeding status on their territory, but usually remain when a helper unrelated to them inherits breeding status. Females also are likely to leave if their mate dies and there are no helpers to assume the breeding vacancy, rather than pair with an immigrant replacement male. This may be a means to avoid young males as mates (Daniels and Walters 2000b, see below). Finally, young females (age 1 or 2) that experience reproductive failure are likely to move (Daniels and Walters 2000b). Like juvenile jumpers, dispersing adult females occasionally move very long distances (Walters et al. 1988b), but typically they move to a neighboring group (Walters et al. 1988a, Daniels 1997).

Reproduction

RCWs are highly monogamous. The breeding male and female within the territory are almost invariably the genetic parents of all offspring (Haig et al. 1993, 1994b). There is no evidence that helpers ever sire offspring, and the frequency of extra-pair fertilization involving individuals outside the group is among the lowest recorded in birds (Haig et al. 1994b).

Typical values of reproductive parameters, and the range of variation among years and populations, are reviewed in Jackson (1994), Conner et al. (2001a) and USFWS (2003). Unless otherwise indicated, values reported here represent a summary of data from these sources. Not all groups attempt nesting in a given year. On average about 10 percent of the groups do not nest, but this ranges from as low as 3% to as high as 21%. Groups with young breeders, especially 1-year-old males, are especially likely to forego nesting (Walters 1990). If the group does nest, the eggs usually are laid in the most recently completed cavity available, which typically is the breeding male's roost cavity (Conner et al. 1998a). If the nest fails, the group may renest. On average about 30% of nest failures are followed by a second attempt, but annual variation in the rate of renesting is high. Rarely a group will make a third nesting attempt following 2 failed nests, or attempt a second brood after a successful first nest (reviewed by Phillips et al. 1998). Equally rare are instances of 2 nests of a single pair in existence at the same time (Rossell and Britcher 1994, Conner et al. 2001b). More frequent, but still uncommon, are instances of 2 females residing together within a group and laying clutches synchronously in a common nest. Usually in such cases one of the females is an unrelated helper that has been present for several years before becoming a co-breeder with the group's breeding female (Walters and Garcia 2016). Such instances are of theoretical interest because they constitute plural breeding, which is characteristic of more complex cooperative breeding systems (Emlen 1991).

Most groups that attempt nesting fledge young, as nest failure rates are low for a species in the temperate zone, although fairly typical for a primary cavity nester (Martin and Liu 1992, Martin 1995). Nest failure rates average about 20%, and this is fairly consistent among years and among populations. Nest predation, nest desertion, and loss of nest cavities to cavity kleptoparasites appear to be the primary causes of nest failure. Failure rate is higher during the egg stage than during the nestling stage, which suggests that nest desertion, rather than nest predation or loss of cavities to kleptoparasites, is the major cause of failure (Ricklefs 1969).

The relative frequencies of the 3 causes of nest loss have not been measured, but much is known about each. Nest predation rates may be lower than in other cavity nesters because of the protection provided by the resin barrier around the cavity (see below), which clearly interferes with climbing by snakes (Rudolph et al. 1990b). The frequency of nest predation may vary regionally, although there is no direct evidence of this. One possibility is that it is higher in areas where most cavities are in species other than longleaf, and thus where the resin barrier is diminished (Conner et al. 1998a), for example in Arkansas (Neal 1992).

In contrast to nest predation, nest desertion may be more common than in other cavity nesters because of the complex social system and resulting intense competition for breeding vacancies characteristic of this species. Lennartz et al. (1987) suggested that nest failure is often associated with repeated territorial intrusions by conspecifics, and other forms of social disruption. Dispersing birds, especially females, often associate with groups as affiliated floaters (Walters et al. 1988a, Walters and Garcia 2016). Such individuals are a particularly likely source of social disruption that might cause groups to forego nesting, or if the groups do attempt to nest, cause nest desertion or even destroy nests (DeLotelle and Epting 1992).

The primary cavity kleptoparasites linked to nest failure are red-bellied woodpeckers (*Melanerpes carolinus*), red-headed woodpeckers (*M. erythrocephalus*), eastern bluebirds (*Sialia sialis*), and southern flying squirrels (*Glaucomys volans*). These species are known to usurp nest cavities from RCWs and to destroy nests in cavities they usurp. Occasionally, red-headed woodpeckers, red-bellied woodpeckers, and flying squirrels may consume eggs and small nestlings (Jackson 1994).

Although RCW groups produce broods fairly reliably, these broods are relatively small. This is because clutch size is modest and, more importantly, because partial brood loss is greater than in other species of primary cavity nesters in the United States (LaBranche and Walters 1994). Most clutches contain 2 to 4 eggs, although the full range is 1 to 5 eggs (Figure 3). Co-breeding females (see above), produce clutches as large as 8 eggs, but more typically 5-7. There is variation among populations in clutch size, with population averages ranging from 2.9 to 3.5 eggs, but there does not appear to be a regular geographic pattern in this variation.

Figure 3. Eggs in natural cavity and 7-8 day old nestlings removed for banding prior to return to cavity.

Incubation begins before the clutch is complete and eggs hatch asynchronously (Ligon 1970). As often occurs in species with asynchronous hatching, partial brood loss occurs soon after hatching (LaBranche and Walters 1994; DeLotelle et al. 2004). Some reduction in brood size is due to failure of eggs to hatch, but much of it is due to mortality of nestlings within the first few days after hatching. Some eggs may fail to hatch because they are infertile. This has been documented to be the primary cause of partial brood loss in one population (Jordan 2002), but this does not appear to be typical. Instead, it appears that most egg loss is due to abandonment of incubation before the last-laid eggs hatch. Similarly, it is the last young to hatch, apparently from starvation, as documented by Sanders (2000) in a study that used video cameras mounted in modified artificial cavities. Sanders (2000) found no evidence of sibling aggression, so it appears improbable that siblicide is a regular component of partial brood loss. Severe aggression among older nestlings has been observed, however. These conflicts presumably are related to acquisition and maintenance of dominance (see below).

Partial brood loss, measured by dividing the number of fledglings by the number of eggs in successful nests, averages about 40%. However, it is highly variable among years and among populations. Partial brood loss tends to be higher in coastal populations compared to inland ones, and in southern populations compared to northern ones (Conner et al. 2001a). Average brood loss in populations vary from around 30% in a northern, inland population (North Carolina Sandhills) to about 50% in a southern, coastal population (Eglin Air Force Base in Florida), and

59% in central Florida.

The number of young fledged from successful nests is typically 1-4. Broods of 5 fledglings occur occasionally in the North Carolina Sandhills at the northern edge of the species' range, whereas the maximum brood size recorded at Eglin Air Force Base, Florida in the southern part of the range is 3 fledglings (Conner et al. 2001a). Because some groups do not nest and others fail in their attempts, the average number of young produced per group is of course fewer, ranging from 0.8 to 1.8 among populations (McKellar et al. 2014). There is considerable annual variation in productivity within populations, and productivity is higher in northern and eastern compared to southern and western populations, and in inland compared to coastal populations (McKellar et al. 2014).

For the first several days after fledging, the young birds are somewhat reluctant to fly, and spend considerable time perched high in the pines, clinging to the trunk or large limbs. Parents and helpers sometimes forage some distance away from the young at this time, but return frequently to feed them (Figure 4). A returning adult targets a particular fledgling and delivers the food it has collected to that individual (Ragheb and Walters 2011). During this initial period, the fledglings often do not return to the cluster with the adults in the evening, but instead roost in the open wherever the adults leave them at the end of the day. The next morning, the adults return and locate the fledglings and resume feeding them.

By the end of the first week out of the nest, however, the young are much more active and move with the adults as the group travels through the territory. There is an abrupt transition between the targeted feedings that characterize the first 9 days after fledging to approach feedings from day 10 onwards (Ragheb and Walters 2011). Fledglings follow adults, beg loudly for food as the adults forage, and quickly approach adults that have captured prey. They may even displace an adult from a particularly productive foraging location. Fledglings are highly aggressive toward one another, and clear dominance hierarchies are evident among siblings. Males, which are recognizable from their red crown patches, are typically dominant to females. Most of the aggression consists of a dominant fledgling displacing a subordinate from an adult that is carrying food or foraging. The fledglings gradually begin to obtain food for themselves, but continue to beg for food and squabble with each other for some time. Young are sometimes observed being fed 2 months after fledging, and are occasionally seen begging as late as the subsequent winter (Ligon 1970).

Figure 4. Adult feeding male nestling at cavity entrance (left) and male fledgling on bole (right).

Gowaty and Lennartz (1985) reported a sex ratio among fledglings biased toward males in a South Carolina population, and Epting and DeLotelle (unpublished) reported a bias toward females in a Florida population. Gowaty and Lennartz (1985) related their results to the local resource enhancement model of Clark (1978), which predicts a bias toward the philopatric sex when that sex contributes to parental fitness, as male helpers do. Emlen et al. (1986) and Lessells and Avery (1987) developed this concept further, terming it the repayment model. Koenig and Walters (1999) applied the repayment model to RCWs and found that the model predicted precisely the male-biased sex ratio observed by Gowaty and Lennartz (1985) in the 2 North Carolina populations they examined. However, the actual sex ratios in these populations, based on a sample size an order of magnitude larger than those studies reporting biased sex ratios, were not significantly different from 50:50 and thus not biased as the model predicted. Thus, it is not clear that there is any bias in offspring sex ratios in RCWs. The sex ratio among adults is, in contrast, male-biased due to higher female mortality associated with the sex differences in philopatry that characterize the social system.

Helpers contribute substantially to both incubating eggs and feeding young, and their presence increases productivity. Groups with helpers produce more young than groups without helpers but this is due in part to an association between the presence of helpers and high territory quality, as well as actual contributions of helpers to reproduction. The best estimate of the helper effect, controlling for effects of territory quality, is that the presence of a helper increases productivity by 0.39 fledglings per group per year, a second helper increases productivity by an additional 0.36 fledglings (Heppell et al. 1994). Productivity does not increase further with addition of more helpers beyond the first two (Walters and Garcia 2016). For unknown reasons, the usual positive effect of helpers on productivity seems to be lacking in two Florida populations (DeLotelle and Epting 1992, Hardesty et al. 1997, but see James et al. 1997).

The mechanism by which helpers increase productivity is not entirely clear. One might assume that since helpers contribute substantially to feeding, groups with helpers should be able to raise larger broods. Indeed, in some cooperative breeders feeding by helpers results in higher provisioning rates and reduced partial brood loss. In others, however, feeding by helpers instead results in reduced feeding effort by the breeders, and positive impacts of helpers are due to reduced nest failure rather than reduced partial brood loss (Emlen 1991). The latter scenario likely characterizes RCWs. Lennartz et al. (1987) reported that groups with helpers on the Francis Marion National Forest experienced both less partial brood loss and less nest failure than groups without helpers. However, older breeders experience less partial brood loss and nest failure (see below), and breeder age is confounded with presence of helpers in Lennartz et al. (1987). Using a much larger sample, and controlling for the age of the female breeder, Reed and Walters (1996) found that in the North Carolina Sandhills higher productivity of groups with helpers was not due to reduced partial brood loss. Instead, groups with helpers were more likely to attempt nesting, and less likely to fail. Khan and Walters (2002) found, in this same population, that feeding by helpers resulted in less feeding by parents rather than more feeding of nestlings.

The age of the breeders strongly affects reproductive success (Walters 1990). Young birds are less successful than old birds, and this is manifested in all components of reproduction. That is, young birds are less likely to attempt nesting, more likely to fail, and suffer more partial brood loss. Productivity of 1-year-old birds of both sexes is especially poor, but reduced productivity is evident through age 3, and the effect is somewhat stronger in males. Ages 4 to 8 are the peak reproductive years, as productivity is reduced somewhat at ages 9 and beyond in both sexes. This may represent senescence.

Mortality

Good estimates of mortality rates are available from completely marked populations or subpopulations, and patterns are clear and consistent (Conner et al. 2001a, USFWS 2003). For a bird of its size residing in temperate regions, the RCW exhibits exceptionally high survival rates. Survival rates of adult male helpers and breeders generally are about 5% higher than that of breeding females. There is distinct geographic variation in survival similar to that observed for partial brood loss. Survival rates are about 75% for males and 70% for females in the northern, inland population in the North Carolina Sandhills, about 80% and 75% respectively in coastal populations in North Carolina, and 86% and 80% , respectively, in the Florida panhandle. Such an association between increased survival and reduced fecundity is common in animal life histories. Annual variation in adult survival within populations is sufficiently small that it can largely be attributed to random chance rather than changes in environmental conditions (Walters et al. 1988a). This level of variation can have large effects in small populations, however, and it appears that in all populations there are occasional poor years in which survival is substantially reduced. Some populations are vulnerable to periodic catastrophic mortality due to hurricanes.

With high survival rates, some individuals live to old ages. A captive female lived to 17 years (J. Jackson, pers. comm.) and the maximum ages recorded for wild birds are 18 for males and 17 for females (Walters, unpublished).

Survival during the first year is more prone to underestimation than survival at subsequent ages, due to the greater possibility of dispersal out of the sampling area. Nevertheless, it is quite clear that survival rates are much lower during the first year than thereafter. In 3 North Carolina populations, survival of males during the first year ranges from 46% to 57%, and of females from 36% to 45% (Conner et al. 2001a). Within a population, survival of males is 10 to 15% higher than survival of females. Survival during the first year is affected by the proportion of individuals dispersing rather than remaining as helpers (dispersing lowers survival), as well as by the physical environment. Thus first-year survival is higher in males and in higher quality habitat (which promotes retention of young as helpers), and has increased over time in both sexes in many populations as habitat has been restored (Walters and Garcia 2016). The effects of habitat and life history on first-year survival make it difficult to detect geographic variation. Nevertheless, there is some evidence that first-year survival is higher in Florida (DeLotelle and Epting 1992).

Differences between age-sex classes suggest that costs of dispersal are a driver of mortality patterns. By regressing survival against the proportion of birds dispersing among various categories of females, Daniels and Walters (2000b) estimated the mortality cost of movement for breeding females in the North Carolina Sandhills at 33%. That is, dispersal between breeding seasons adds another 33% to the probability of mortality above that of site-faithful birds. Specifically, the expected survival rate for females that do not move is 74%, whereas that for females that do move is 41%. This is a surprisingly high cost, given the short distances that most individuals move. This result may reflect the intensity of competition for breeding vacancies, the benefits of belonging to a group, or perhaps the benefits of ready access to a suitable roost cavity.

Overall, the mortality pattern is typical of cooperatively breeding avian species. It is characterized by relatively low survival during the first year, especially of dispersers; relatively high survival of breeders and helpers; and senescence at the end of the life span. Compared to non-cooperative species, survival of both juveniles and adults is high, and the life span is long.

Foraging Ecology

Our understanding of the foraging ecology of RCWs is increasing, although much work remains to be done. Natural geographic variation in forest ecology and woodpecker demography as well as the highly altered structure of today's forests make documenting habitat preferences and requirements a complex and challenging task. Despite these difficulties, an informative body of research describing foraging ecology and habitat relationships of RCWs exists. Here, we summarize research into diet, habitat selection, and habitat effects on fitness.

Diet of Adults and Nestlings

Over 75% of the diet of RCWs consists of arthropods, especially ants and cockroaches, but also beetles, spiders, centipedes, true bugs, crickets, and moths (Beal et al. 1941, Baker 1971a, Harlow and Lennartz 1977, Hanula and Franzreb 1995, Hess and James 1998, Hanula and Engstrom 2000, Hanula et al. 2000b). Ants are particularly common in stomach content samples, comprising over half the items in such samples of adults and sub-adults in the Gulf coast region (Beal et al. 1941) and the Apalachicola National Forest in Florida (Hess and James 1998). Other arthropods comprised an estimated 34% and 17%, respectively, of the adult diet in these two studies (Beal *et al.* 1941, Hess and James 1998). *Crematogaster ashmeadii* was the most prominent of the ant species in the stomachs of RCWs in the Apalachicola, comprising 74% of the ant biomass (Hess and James 1998). Stomach samples of diet are biased toward components such as ant exoskeletons that preserve well. Recent preliminary analysis using a new method that produces unbiased samples of diet indicate that the diet of RCWs is much more varied, and less dependent on ants, than earlier stomach sample analyses suggest (M. Jusino, unpublished).

Fruits and seeds make up a small portion of the adult diet. RCWs have been known to eat the fruits or seeds of pines (*Pinus spp.*), poison ivy (*Rhus radicans*), magnolia (*Magnolia spp.*), wax myrtle (*Myrica spp.*), wild cherry (*Prunus serotina*), wild grape (*Vitus spp.*), blueberry (*Vaccinum spp.*), and blackgum (*Nyssa sylvatica*). Fruits and seeds comprised 14% by volume of the stomach contents of adults collected throughout the year in the Gulf Coastal Plain (Beal et al. 1941). Similarly, fruits and seeds made up 16% of the stomach contents of adults in Apalachicola National Forest (Hess and James 1998). Plant material was rare in the diets of RCWs in the Francis Marion National Forest of South Carolina (Hooper and Lennartz 1981).

The diet of nestlings also consists principally of arthropods, with fruits being a minor component (Baker 1971a, Harlow and Lennartz 1977, Hanula and Engstrom 2000, Hanula et al. 2000b). Large arthropod prey are commonly fed to nestlings in addition to or instead of ants (Hanula and Franzreb 1995, Hess and James 1998, Hanula and Engstrom 2000, Hanula et al. 2000b), and there is some evidence that breeding groups increase their reproductive success by feeding large prey (Schaefer 1996). In the Apalachicola National Forest, the diet of nestlings (as estimated by stomach contents) consisted mainly of roughly equal proportions of ants, beetles, spiders, and centipedes (Hess and James 1998). In several populations in Georgia and South Carolina, wood roaches were the most common item fed to nestlings, comprising from 26 to 62 percent of the nestling diet (as estimated from photographs of feeding visits; Hanula and Franzreb 1995, Hanula and Engstrom 2000, Hanula et al. 2000b).

Prey Selection, Location, and Abundance

RCWs generally capture arthropods on and under the outer bark of live pines and in dead branches of live pines (Figure 5). Pines that have recently died are also a notable source of prey (Ligon 1968, Hooper and Lennartz 1981, Schaefer 1996, Bowman et al. 1997). RCWs rarely excavate through the bark of live pines to capture prey, but do excavate into dead branches (Ligon 1968, Ramey 1980, Hooper and Lennartz 1981, Porter and Labisky 1986, Schaefer 1996).

Differences in foraging behavior between the sexes are well documented (Ligon 1970, Hooper and Lennartz 1981, Engstrom and Sanders 1997, Hardesty et al. 1997). Males commonly forage on limbs and twigs, rarely forage on the lower trunk, and are often on dead branches. Females commonly forage on the lower trunk, and rarely forage on limbs, twigs or dead branches. This difference may result from intersexual competition, with the dominant males maintaining access to the best foraging areas, as occurs in downy woodpeckers. More likely, foraging differences may represent niche dimorphism that reduces intersexual competition within family groups, with each sex foraging in the part of the tree to which they are best adapted. The longer legs of males might be an adaptation to foraging more on limbs and twigs, whereas the longer tails of females may be an adaptation to foraging on the trunk (Pizzoni-Ardemani 1990). Foraging behavior may differ by social status as well as sex, at least among males: in east Texas breeding males spend more time in the inner crown of the tree, whereas helper males forage more on the outer branches (Conner et al. 2001a).

Figure 5. RCWs foraging on pine.

Several studies have assessed abundance and location of potential prey of RCWs (Hooper 1996, Hanula and Franzreb 1998, Hess and James 1998, Hanula et al. 2000a). Relative abundance of arthropods changes depending on the part of the tree sampled. On the boles of the tree, the most abundant arthropods were true bugs, spiders, and roaches (Hooper 1996). On live branches, roaches, spiders, beetles and ants were most common (Hooper 1996); ants appear to be by far the most common arthropod on dead branches (Hooper 1996, Hanula and Franzreb 1998). A large proportion of the arthropods on pine trees have gotten there by crawling up from the ground, which points to the condition of the ground cover as an important factor influencing abundance of prey for RCWs (Collins et al. 1998, Hanula and Franzreb 1998). This may account for the correlation between productivity of RCW groups and the condition of the ground cover in their territories (see below).

Thus, several studies have documented a variety of arthropod species in the diet of RCWs, and others have described patterns of arthropod abundance and distribution. Whether birds are selecting prey species in greater proportion than their availability remains unknown. Assessing prey selection is extremely difficult, in large part because of variability in the distribution of arthropods over time and space that makes it virtually impossible to sample availability at the scale of RCW territories, and also because of biases in the methods for sampling diets.

Nesting Habitat

RCWs require open pine woodlands and savannahs with large old pines for nesting and roosting. Old pines are required as cavity trees because cavity chambers must be completely within the heartwood to prevent pine resin in the sapwood from entering the chamber (Jackson and Jackson 1986, Clark 1993), and because heartwood diameter is a function of tree age (Conner et al. 2001a). In addition, old pines have a higher incidence of the heartwood decay that greatly facilitates cavity excavation (see below). Cavity trees, with rare exception, must be in open stands with little or no hardwood midstory and few or no overstory hardwoods. Hardwood encroachment on cavity trees resulting from fire suppression is a well-known cause of cluster abandonment.

There is geographic variation in nesting and roosting habitat of RCWs. The largest populations tend to occur in the core of the range, the primarily longleaf pine woodlands and savannahs of the Coastal Plains and Carolina Sandhills (Carter 1971, Hooper *et al.* 1982, James 1995, Engstrom et al. 1996). The shortleaf/loblolly (*Pinus echinata/P. taeda*) forests of the Piedmont, Cumberlands, Ouachita Mountain regions (Mengel 1965, Sutton 1967, Steirly 1973), east Texas, and the upper Gulf Coastal Plain is another important habitat type. In southern Florida, south Florida slash pine (*P. elliottii* var. *densa*), particularly south of the natural range of longleaf pine, is an important type. RCWs occupy a variety of additional pine habitat types, and excavate cavities in additional pine species, at the edges of their range, including slash, pond, pitch (*P. rigida*), and Virginia pines (*P. virginiana*; Steirly 1957, Lowery 1960, Mengel 1965, Sutton 1967, Hopkins and Lynn 1971, Jackson 1971, Murphy 1982). Where multiple pine species exist, longleaf pine appears to be preferred (Lowery 1960, Hopkins and Lynn 1971, Jackson 1971, Baker 1981, Bowman et al. 1997).

Cavities

RCWS are unique among North American woodpeckers in that they nest and roost in cavities they excavate in living pines (Steirly 1957, Short 1982, Ligon et al. 1986). This unusual behavior may have evolved in response to the scarcity of snags and hardwoods in the fire-maintained pine ecosystems of the Southeast (Ligon 1970, Jackson et al. 1986). Excavation of cavities in live pines has given rise to additional unusual and complex behaviors, ranging from cooperative breeding (Walters et al. 1992a) to daily excavation of resin wells to create resin barriers against predatory North American rat snakes (*Pantherophis sp.,* Ligon 1970, Dennis 1971b, Jackson 1974, 1978a, Rudolph *et al.* 1990b). Use of live pines is also the primary reason why the species requires mature pines, the loss of which has resulted in endangerment.

Cavities are an essential resource for RCWs throughout the year, because the birds use them for roosting year-round, as well as nesting seasonally. Each individual in a group has its own roost cavity and the group usually nests in the breeding male's cavity. The aggregation of active (in use) and inactive (previously used) cavity trees within the area defended by a single group is termed the cavity tree cluster (Walters et al. 1988a). This aggregation of cavity trees is dynamic, changing in shape as new cavity trees are added through excavation and existing cavity trees are lost to death or a neighboring group. To facilitate record keeping and protection, individual cavity trees within a cluster are commonly marked with metal numbered tags, painted for easy detection, and mapped.

Cavity Excavation

Excavation of cavities in live pines is an amazingly difficult task (Figure 6). Birds must first select a suitable old pine (Jackson and Jackson 1986, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Rudolph and Conner 1991), then excavate an entrance tunnel through 10 to 15 cm (4 to 6 in) of live sapwood, avoiding dangerous pine resin that seeps from the wood, and finally construct a cavity chamber within the heartwood (Jackson 1977, Hooper et al. 1980, Conner and Locke 1982, Conner and O'Halloran 1987, Hooper 1988, Hooper et al. 1991). The time required to excavate a cavity varies greatly, but excavation typically takes many years (Jackson et al. 1979, Rudolph and Conner 1991, Conner and Rudolph 1995a). Most studies underestimate excavation time because they include only cavities excavated to completion and thus are biased against long excavation times. In the only study to base estimates on partially completed as well as complete cavities, estimated excavation times in 3 North Carolina populations were 10-13 years in longleaf pine and 6-9 years in loblolly pine (Harding and Walters 2002). Progress is especially slow when excavating in sapwood. At this stage, the birds excavate only in the warm summer months, and will sometimes cease excavating for a month to several years, to allow resin flow to subside through resinosis (saturation of sapwood with hardened resin; Conner and Rudolph 1995a).

Figure 6. Initial cavity start in outer sapwood (A), cavity entrance in sapwood (B), completed cavity with resin wells (C), and longitudinal section of completed cavity thru entrance and chamber (D).

As in North Carolina, cavity excavation times in Texas, estimated from a sample of completed cavities, were longer in longleaf pines than in either loblolly or shortleaf pines. Excavation time averaged 6.3 years in longleaf pines, two to three times greater than the average times for loblolly and shortleaf pines (Conner and Rudolph 1995a). Presumably, longleaf requires longer excavation times because of its greater resin flow (see below). Geographic variation in resin flow, as well as pine species used, likely contributes to variation in excavation times (Hodges et al. 1979, Ross et al. 1995).

The difficulty of cavity excavation is considered a major factor in the evolution of cooperative breeding in RCWs (Walters 1991, Walters et al. 1992a, 1992b). Birds cannot easily exploit previously unoccupied habitat and build new cavity tree clusters, so instead compete for territories with existing cavities. Under these conditions of intense competition, delaying reproduction and remaining on the natal territory while awaiting a breeding opportunity on an existing territory is a viable pathway to high lifetime fitness (Walters 1990, Walters and Garcia 2016, Walters *et al.* 1988a, 1992b). Accordingly, natural formation of groups in previously unoccupied habitat (pioneering, Hooper 1983) is rare; its estimated annual rate is less than 3% of total groups in a population under current conditions (Walters 1990).

RCWs are able to exploit the resin of the live pine to protect against predation of nests and adults by arboreal snakes (Ligon 1970, Dennis 1971b, Jackson 1974, 1978a, Rudolph et al. 1990b). The birds create and maintain resin wells, or wounds in the cambium, to coat the trunk with resin that effectively interferes with the snakes' ability to climb the tree (Rudolph et al. 1990b). The birds chip away at the resin wells on their cavity trees daily, enabling one to distinguish cavities that are currently in use by the presence of fresh resin.

Longleaf pine may be preferred for use as cavity trees because it produces more resin and can sustain resin flow for more years than other southern pines (Wahlenburg 1946, Hodges et al. 1977, 1979, Bowman and Huh 1995, Ross et al. 1995). The production of more resin affords the birds greater protection against snakes and also provides the tree with greater protection against insects such as southern pine beetles (Hodges et al. 1979). Annual survival of longleaf cavity trees was twice that for loblolly and shortleaf cavity trees in east Texas, in part because of longleaf pine's greater resistance to southern pine beetles (Conner and Rudolph 1995a). Because of higher survival and the ability to sustain resin flow over time, longleaf pines may remain in use as cavity trees for several decades—much longer than shortleaf or loblolly pines (Conner and Rudolph 1995a, Harding 1997).

Cavity Tree Selection

RCWs select and require old pines for cavity excavation (Jackson and Jackson 1986, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Rudolph and Conner 1991). Age of cavity trees depends on the ages of pines available, but there is a minimum age, generally 60 to 80 years depending on tree and site factors, below which use as a cavity tree is highly unlikely or simply not possible (DeLotelle and Epting 1988, Hooper 1988, Rudolph and Conner 1991). Old growth pines are relatively rare throughout the Southeast, and old growth remnants (both single trees and stands) within today's forests are critically important and will continue to be so until second growth forests mature sufficiently that potential cavity trees become more widely available. Cavity trees are generally the oldest trees available in today's forests (Jackson et al. 1979, Engstrom and Evans 1990, Rudolph and Conner 1991), and the birds continue to select the oldest trees available for initiation of cavities (Rudolph and Conner 1991). Only in the last 10 years, and only in some populations, have the birds begun to excavate regularly in second-growth trees rather than remnant old growth trees. Nevertheless, the optimal age for cavity trees remains well above the average age of cavity trees in current forests.

One reason RCWs require old trees for cavity excavation is that they need sufficient heartwood diameter at preferred cavity heights to construct the cavity completely within the heartwood. The estimated minimum amount of heartwood required is 14.0 to 15.2 cm (5.5 to 6 inches; Conner et al. 1994). Preferred cavity heights generally range from 6.1 to 15.2 m (20 to 50 ft; Baker 1971b, Hopkins and Lynn 1971, Hooper et al. 1980, Conner and O'Halloran 1987), a possible adaptation to minimize likelihood of ignition by frequent fire (Conner and O'Halloran 1987, Clark 1992, Conner et al. 1994). The age of the tree determines heartwood diameter at cavity height, as older pines have more heartwood at greater heights. In eastern Texas, longleaf pines between 70 and 90 years old had adequate heartwood at appropriate heights to contain a cavity (Conner et al. 1994). Fifty year-old longleaf pines examined by Clark (1992) had insufficient heartwood for cavity excavation.

A second reason that RCWs select old trees for cavity excavation is that old pines have a higher frequency of infection by fungus and the associated decay of the heartwood becomes more advanced as the tree ages (Wahlenburg 1946). Most research on the role of fungi in cavity tree selection and cavity excavation has focused on one species, red heart fungus (*Porodaelalea pini*, formerly *Phellinus pini*). RCWs can and do excavate cavities into undecayed heartwood (Beckett 1971, Conner and Locke 1982, Hooper 1988, Hooper et al. 1991), but the presence of red heart fungus can substantially reduce the time required for cavity excavation (Conner and Rudolph 1995a). In Texas, for example, average excavation times for cavities in pines with and without decayed heartwood were 3.7 and 5 years, respectively (Conner and Rudolph 1995a). RCWs actively select pines with heartwood decayed by red heart fungus (Steirly 1957, Jackson 1977, Conner and Locke 1982, Hooper 1988, Hooper et al. 1991, Rudolph et al. 1995), and in fact are able to detect and locate cavities in the specific area of the bole that is infected (Rudolph et al. 1995).

Preference for decayed heartwood results in the selection of cavity trees that are older than necessary for them to have enough heartwood to contain a cavity (Hooper 1988, Hooper et al. 1991, Rudolph et al. 1995). For example, cavity trees in Texas averaged 24.8 cm (9.75 in) in heartwood diameter, considerably larger than the 15.2 cm (6 in) estimated minimum (Rudolph et al. 1995). Heartwood decay by red heart fungus was not frequently found in longleaf cavity trees in Texas until they were over 120 years old (Conner *et al.* 1994). Red heart is a very slow growing fungus (Affeltranger 1971, Conner and Locke 1982, 1983), and 12 to 20 years may be required between initial inoculation and the decay of sufficient heartwood to house a cavity (Conner and Locke 1983). Because red heart fungus enters the heartwood of the tree through exposed heartwood in large, broken branches, trees must be old enough to have large branches before bole heartwood can be infected (Affeltranger 1971, Conner and Locke 1982). Regional differences may exist in the ages and rates at which pines become infected with heartwood decaying fungi. A study in Texas reported a 46% infection rate for 50 longleaf cavity trees that averaged 126 years in age (Conner et al. 1994), whereas this rate was more than double for similarly aged longleaf cavity trees in South Carolina (97% infection rate for trees averaging 130 years in age; Hooper 1988).

Recent work has revealed that red heart fungus is not the only fungus involved in cavity excavation by RCWs, and that the interaction between the birds and the fungi is more complicated than previously thought. Jusino et al. (2015) demonstrated a community of fungi in natural and artificial excavations that undergoes a process of succession toward the community found in completed cavities as excavation proceeds. Excavations from which birds are excluded develop a different fungal community than that found in excavations the birds use, suggesting that RCWs either inoculate their excavations with particular fungi or somehow influence community succession to favor particular fungi (Jusino et al. 2015). Thus, cavity excavation involves a symbiotic relationship between RCWs and particular wood-rotting fungi, including *P. pini,* in which RCW cavity excavations facilitate fungal colonization. The spores of the fungi involved are found on the bodies of the birds (Jusino et al. 2016). Previous understanding of cavity tree selection based on red heart fungus alone needs to be reexamined in light of these new discoveries.

RCWs select pines that have thinner sapwood and greater heartwood diameters than pines generally available nearby (Conner et al. 1994). This too is related to age: such trees are older, grow more slowly, and usually have a higher rate of red heart infection than pines not used for cavity excavation. Excavation through the sapwood into the heartwood can proceed more quickly in such trees.

RCWs select trees that have higher resin flow than surrounding pines for cavity excavation (Bowman and Huh 1995, Conner et al. 1998a). Moreover, breeding males select the cavity tree with the highest resin flow for use as the nest tree (Conner et al. 1998a). Ross et al. (1997) showed that longleaf pine cavity trees in stands with low densities and on forest edges produced significantly more resin than similar cavity trees within interior forest stands with higher stem densities. Several studies have observed the tendency of RCWs to place their cavities near forest edges and in areas of low tree densities (Conner and O’Halloran 1987, Conner et al. 1991b, Ross *et al.* 1997), presumably because of higher resin flow of trees in these locations.

Nesting Habitat Selection

Alteration of the natural fire regime during the previous century caused fundamental changes in the vegetation structure of upland habitats throughout the Southeast. These changes include a gradual encroachment of fire intolerant hardwoods, increasing dominance of off-site pine species such as slash and loblolly, and more densely wooded forests in general (Jackson et al. 1986, Ware et al. 1993). Loblolly pine was present historically, but forests dominated by loblolly were very rare; its presence and dominance has increased dramatically due to fire suppression (White 1984). Each of these changes is detrimental to RCWs, and hardwood encroachment on pine habitats especially is a major cause of the species' decline and endangered status.

The association of RCWs with open, park-like pine habitats has long been known (Thompson and Baker 1971, Van Balen and Doerr 1978, Locke et al. 1983, USFWS 1985). Encroachment of hardwood midstory on cavity trees causes abandonment of individual cavities and cavity tree clusters (Beckett 1971, Hopkins and Lynn 1971, Van Balen and Doerr 1978, Locke et al. 1983, Hovis and Labisky 1985, Conner and Rudolph 1989, Loeb et al. 1992). Cluster abandonment has been documented when hardwood and pine midstory basal area exceeds 5.7 m^2/ha (25 ft^2/acre; Conner and Rudolph 1989, Loeb et al. 1992), and midstory height exceeds 3.7 m (12 ft) (Hooper et al. 1980).

Thus, effective midstory control in cavity tree clusters is an absolute prerequisite to management, conservation, and recovery of RCWs throughout their range. Such control is not an easy task. After 7 decades of fire suppression, many clusters developed an extensive hardwood component with an impressive underground root stock, particularly in the more mesic sites where loblolly and shortleaf pines are the dominant tree species (Conner and Rudolph 1989). Repeated prescribed burning during the late dormant or early growing season is an effective means to remove hardwoods and restore native groundcovers, and has the least detrimental impacts on soil structure and desired groundcovers (Provencher et al. 2001a, 2001b). However, excessive quantities of hardwoods (or very large trees) may require removal by hand, mechanical means (Conner et al. 1995), one-time herbicide application (Conner 1989), or a combination of these methods prior to restoration burning. Chemical and/or mechanical techniques may be useful if rapid midstory reduction is required, for example, if a cluster has been recently abandoned or supports only a solitary male because of excessive hardwoods. If chemical and/or mechanical techniques are used, it is important that regular prescribed burning follows these treatments.

Habitat in RCW clusters has been successfully restored to an open condition in many populations over the past 2 decades. Although work remains to be done, maintenance of habitat is the primary management need in many populations. Maintenance of open habitat structure once restored is best achieved through regular prescribed fire fueled by native grasses and pine needle litter. The greatest management challenges in these cases are factors such as funding, sufficient personnel, urban encroachment and smoke management that constrain ability to burn restored areas at the frequency necessary to maintain desired conditions.

RCWs can tolerate some hardwood overstory trees (basal area less than 2.3 m^2/ha; 10 ft^2/ac) within clusters (Hooper et al. 1980, Hovis and Labisky 1985, Conner and O’Halloran 1987). Small numbers of overstory hardwoods or large midstory hardwoods at low densities are consistent with historic landscapes in many habitats and do not have the same negative effects on RCWs as the dense hardwood midstories resulting from fire suppression (Hiers et al. 2007). Oak inclusions and upland hardwood species, such as post oak (*Quercus stellata*) and bluejack oak (*Q. incana*), occur naturally in association with the pine ecosystems of the Southeast. Such species are integral components of the southern pine ecosystem and should not be eliminated in the name of RCW management (Hiers et al. 2007).

Density of pines in clusters varies according to habitat type, geography, and silvicultural history. The sparsest habitat occupied by RCWs are the hydric slash pine woodlands of south Florida (Beever and Dryden 1992). Slightly more dense are the clusters in longleaf woodlands of south and central Florida; average basal area of clusters in these Florida longleaf woodlands currently ranges from 1.8 to 5.7 m^2/ha (8 to 25 ft^2/ac; DeLotelle et al. 1983, Shapiro 1983, Hovis and Labisky 1985, Bowman et al. 1997). For clusters in longleaf pine woodlands north of Florida, estimated average basal area ranges from 9.2 to 13.8 m^2/ha (40 to 60 ft^2/ac) of basal area (Crosby 1971, Hopkins and Lynn 1971, Thompson and Baker 1971). Clusters in natural loblolly and/or shortleaf pine forests average slightly higher densities (Thompson and Baker 1971, Hooper et al. 1980, Conner and O'Halloran 1987, Conner and Rudolph 1989).

RCW clusters typically are located in pine stands that are less dense than surrounding stands (Crosby 1971, Thompson and Baker 1971, Grimes 1977, Locke et al. 1983, Shapiro 1983, Wood 1983, Hovis and Labisky 1985, Conner and O'Halloran 1987, Conner et al. 1991b, Loeb et al. 1992, Bowman et al. 1997) and they may be the least dense stands available. For example, Conner et al. (1991b) reported a preference for seed-tree and shelterwood cuts adjacent to dense fire-suppressed stands for cavity excavation in longleaf pine woodlands, although tree mortality was high in the sparse seed-tree and shelterwoods due to windthrow and lightning. For clusters, basal areas as low as 9.2 m^2/ha (40 ft^2/ac) in longleaf stands and from 9.2 to 13.8 m^2/ha (40 to 60 ft^2/ac) in shortleaf/loblolly stands are suitable (Conner et al. 1991b). However, seed-tree and shelterwood cuts with excessive pine or hardwood midstory are not acceptable as nesting habitat.

There are several reasons why RCWs might select stands with relatively low pine density as cluster sites. Pines in low-density stands grow larger in diameter, have greater crowns and root systems, and higher resin flow. Such pines are more resistant to wind damage and attacks by bark beetles, they may be used as cavity trees at younger ages, and they provide the birds with greater protection against predation. In addition, sparse woods may have a greater proportion of area in grass and forb groundcovers than more dense forests, and these groundcovers in turn affect arthropod abundance (Collins 1998) and the ability of the stand to carry fire. Another reason for the preference for sparsely wooded stands, apart from the above benefits, may be that the low density of pine itself is a reflection of frequent fire.

Cavity Tree Mortality and Protection

Southern Pine Beetles

Infestation by southern pine beetles is the major cause of cavity tree mortality in loblolly and shortleaf pines (Conner et al. 1991a). Cavity trees are lost to southern pine beetles during epidemics, such as the death of 350 cavity trees including more than 50 entire clusters during the early 1980s in the Sam Houston National Forest (Conner et al. 1991a, 1997a). Cavity trees are also lost to southern pine beetles at endemic population levels, at a lower but steady rate (Conner et al. 1997a). Loss of cavity trees resulting from both epidemic and endemic southern pine beetles can substantially impact RCWs, particularly small populations in the loblolly and shortleaf pines of Texas, Arkansas, Louisiana, Mississippi, and elsewhere (Conner and Rudolph 1995b, Rudolph and Conner 1995). Factors that increase risk to cavity trees and other important, mature pines in the cluster to southern pine beetle infestation include physical disturbance of soils and roots during thinning and midstory reduction, high density of pines within the cluster, excessive hardwood midstory outside the cluster, and pine stress due to drought, water saturated soil, extreme fire, and other factors(Thatcher et al. 1980, Nebeker and Hodges 1985, Hicks et al. 1987, Conner et al. 1997a).

Fortunately, pines with artificial cavities, used to mitigate losses of cavity trees to southern pine beetles, are not infested at a rate significantly different from pines with naturally excavated cavities (Conner et al. 1998b). Risk of beetle infestation of trees in which artificial cavities are constructed can be reduced by favoring pines with high resin producing ability, by pine thinning, and by minimizing disturbance during periods of high beetle activity (Mitchell et al. 1991). Loblolly and shortleaf pine stands should be maintained at basal areas less than 18.4 m^2/ha (80 ft^2/ac) or an average spacing of at least 7.6 m (25 ft) between pines in mature stands, to retard the spread of beetle infestations (Thatcher et al. 1980, Hicks et al. 1987, Nebeker and Hodges 1985, Mitchell et al. 1991).

For southern pines, defense against bark beetle attack is positively related to the trees' ability to produce oleoresins (Lorio 1986). Because of differences in resin production, longleaf pines are much less susceptible to beetle attack than loblolly and shortleaf pines, and shortleaf pines are less susceptible than loblolly. Pine beetles are not a significant threat to longleaf pine, occasionally killing individual trees (often trees already stressed by other factors) but not causing epidemics. This may be another reason RCWs prefer longleaf to other pines for cavity excavation.

Other Causes of Mortality

Wind is another major cause of cavity tree mortality (Conner et al. 1991a). Cavity trees can be uprooted or snapped at the cavity by high velocity winds. Patterns of harvest near clusters should be carefully planned to avoid funneling wind toward cavity trees (Conner et al. 1991a, Conner and Rudolph 1995c). A forest buffer of uncut trees greater than 61 m (200 ft) wide around cavity trees is adequate protection to minimize wind damage, wind snap, and wind throw during isolated severe summer thunderstorms (Conner and Rudolph 1995c).

Hurricane winds are a major threat to coastal RCW populations (Engstrom and Evans 1990, Hooper et al. 1990, Hooper and McAdie 1995, Lipscomb and Williams 1995). When Hurricane Hugo struck the Francis Marion National Forests in South Carolina during September 1989, it destroyed 87% of the cavity trees, 67% of the woodpeckers, and 70% of the foraging habitat (Hooper et al. 1990, Hooper and McAdie 1995). Drilled and inserted artificial cavities (Copeyon

1990, Allen 1991, Taylor and Hooper 1991), having just been developed, enabled the rapid recovery of the Francis Marion population (Watson et al. 1995). Hooper and McAdie (1995) suggested that pines needed for future nesting habitat be grown in open conditions to promote the development of large crowns, extensive root systems, and strong boles. Another strategy to minimize impacts from hurricane winds is to avoid the creation of openings greater than 10.1 ha (25 ac) in or near habitat managed for RCWs in hurricane-prone areas. The wind access to forest stands created by the checkboard pattern of timber harvest in the Francis Marion National Forest likely contributed to the extent of damage wrought by Hurricane Hugo.

The third major cause of cavity tree mortality is fire. Managers must take appropriate measures to protect cavity trees from prescribed burns and wildfires so that loss is minimized. Foremost among these protective measures is regular burning within the cluster and around cavity trees to keep fuel at acceptable levels.

Foraging Habitat

RCWs also require abundant foraging habitat. Suitable foraging habitat generally consists of mature pines with an open canopy, low densities of small pines, a sparse hardwood and/or pine midstory, few or no overstory hardwoods, and abundant native bunchgrass and forb groundcovers. Pine habitat occupied by RCWs covers a wide moisture gradient ranging from hydric slash pine (*P. elliottii* var. *densa)* flatwoods in Florida (Beever and Dryden 1992, Bowman and Huh 1995) and pocosins and swamp forests in northeastern North Carolina (Carter and Brust 2004), to dry ridge and mountaintops in Oklahoma (Masters et al. 1989, Kelly et al. 1993), Alabama, and Mississippi and xeric pine uplands in the Florida panhandle. The nature and density of the ground cover and midstory vary with moisture gradient. Density of pine overstory in areas occupied by RCWs varies from fairly dense in Texas (Conner and O'Halloran 1987, Conner and Rudolph 1989), to sparse in the Orlando, Florida vicinity (DeLotelle et al. 1987), to extremely low in the Big Cypress National Preserve (Patterson and Robertson 1981).

RCWs show a strong preference for living pines as foraging substrate (Hooper and Lennartz 1981, Porter and Labisky 1986, Jones 1994, Bowman et al. 1997). Pines used for foraging include longleaf, slash, loblolly, shortleaf, Virginia, and pond. Sand pine may be used rarely (Hardesty *et al.* 1997), and cypress is used on occasion, averaging an estimated 10% of foraging time in south-central Florida (Nesbitt et al. 1978, DeLotelle et al. 1983). Hardwoods are used on occasion (Hooper and Lennartz 1981, Repasky 1984, Porter and Labisky 1986, Bradshaw 1995, Jones 1994, Hardesty et al. 1997, Zenitsky 1999), but comprise a trivial or minor component of foraging substrate for RCWs throughout their range.

Dying and recently dead pines are an important foraging resource for RCWs (Ligon 1968, Hooper and Lennartz 1981, Schaefer 1996, Bowman et al. 1997, Schaefer et al. 2004). Pines infested with or recently killed and vacated by southern pine beetles may be an especially important, though unpredictable, food source in shortleaf and loblolly habitats (Schaefer 1996). RCWs feed on southern pine beetles themselves, especially pupae in the bark. The birds also feed on adults and larvae of secondary attackers to beetle-infested trees, such as long-horned beetles (*Cerambycidae*) and metallic wood-boring beetles (*Buprestidae*).

Arthropod abundance and biomass increases with the age and size of pines (Hooper 1996, Hanula et al. 2000a). Whether this relationship continues to increase with age, or levels off and declines at some threshold age is unknown. Hanula et al. (2000a) found that arthropod abundance per tree increased linearly with stand age, and that biomass per tree increased until approximately age 60 after which it began to decline. This study showed a similar, positive relationship between arthropods and tree diameter, and negative relationships between density of pines and arthropod abundance and biomass per tree. The negative relationship to density likely is due at least in part to the negative effect of pine density on ground cover, from which some of the arthropod prey comes (see below). It is not yet clear which factors—size, age, and/or density—are more important in determining arthropod abundance and distribution.

Fire frequency also affects arthropod abundance and diversity. Large-scale, well-replicated research into longleaf pine ecosystem restoration in Florida documented increases in densities of herb-layer arthropods in response to prescribed burning, and proposed their use as indicators of restoration success (Provencher et al. 2001a). In Texas, the abundance of arthropods on the boles of shortleaf and loblolly pines was higher in stands with grass and forb groundcover than in stands with substantial hardwood midstory (Collins 1998). Hanula et al. (2000a) documented positive relationships between tree age and the abundance of both herbaceous groundcovers and insects, although there were no direct relationships between measures of herb and insect abundance.

Frequent fire likely increases foraging habitat quality through more than one mechanism, first, by reducing hardwoods, and secondly, by increasing abundance and perhaps nutrient value of prey (James et al. 1997, Provencher et al. 1998, but see Hanula et al. 2000b). The increase in insect abundance is at least partially independent of the reduction in hardwoods. James et al. (1997) revealed this independence by showing an effect of fire on fitness in a study area that had few hardwoods. Provencher et al. (1998) documented 2 to 7-fold increases in insect densities following growing season fire of hardwood-encroached longleaf stands. They then showed that reductions in hardwoods by herbicides and mechanical felling did not result in similar increases in insect densities until the stands were burned during the growing season (Provencher et al. 2001a). Thus, frequent growing season fire may be critically important in providing RCWs with abundant prey.

Geographic Variation in Foraging Habitat

Considerable geographic variation in habitat types exists, illustrating the species' ability to adapt to a wide range of ecological conditions within the constraints of mature or old growth, southern pine ecosystems. RCWs inhabit longleaf pine savannahs, flatwoods, sandhills, and clayhills; slash pine savannahs and flatwoods; pond and/or slash pine pocosins; shortleaf pine savannahs and forests; and shortleaf/loblolly pine savannahs and forests (Nesbitt et al. 1978, Ramey 1980, DeLotelle et al. 1983, Hooper and Harlow 1986, Porter and Labisky 1986, Bradshaw 1995, Epting et al. 1995, Bowman et al. 1997). RCWs also use loblolly pine forests, although historically pure stands of loblolly were rare (White 1984). Longleaf pine ecosystems provide the optimal habitat for RCWs (Conner et al. 2001a).

Historically, longleaf pine ecosystems were the most common habitat type, and they still support most of the largest remaining populations (Carter et al. 1983, Hooper et al. 1982, James 1995, Engstrom et al. 1996). Within these longleaf pine habitats, there is natural community variation in structure and species composition in response to soil type, moisture, nutrients and topographic position (Peet 2006, Carr et al. 2009). RCWs also exist in other habitat types including shortleaf pine communities of Arkansas and Oklahoma (Wood 1983, Masters et al. 1989, Kelly et al. 1993, Hines and Kalisz 1995, Zenitsky 1999), transitional zones of the Piedmont (Steirly 1957), wet loblolly and pond pine communities of northeastern North Carolina (Carter and Burst 2004, Smith et al. 2018b), native hydric south Florida slash pine system of south Florida (Beever and Dryden 1992), and loblolly forests in many areas (e.g., Hooper and Harlow 1986).

Longleaf Pine Communities

Intact longleaf pine communities with frequent low-intensity fire are floristically diverse bilayered communities with an open overstory above a species rich herbaceous ground layer. Plant species richness can exceed 40 or more per square meter within some longleaf community types (Peet and Allard 1993). Floristically, at least 1000 species are obligates of longleaf pine communities (Sorrie and Weakley 2006). Longleaf pine communities vary in response to plant species composition, soil moisture, nutrients, topography, biogeography, and fire and wind disturbance factors (Gilliam et al. 2006, Peet 2006, Carr et al. 2009). A variety of longleaf pine community classifications have been developed in response to these patterns of diversity. The classification by Peet (2006) is based primarily on variation in longleaf vegetation to soil moisture and texture across 6 ecoregions (Figure 7). Up to six broad ecological groups occur within each Region (Table 1): xeric sand barrens and uplands, subxeric sandy uplands, silty uplands, clayey and rocky uplands, flatwoods, and savannas and seeps. Each of these groups includes a large number of distinct vegetation associations further described by Peet (2006).

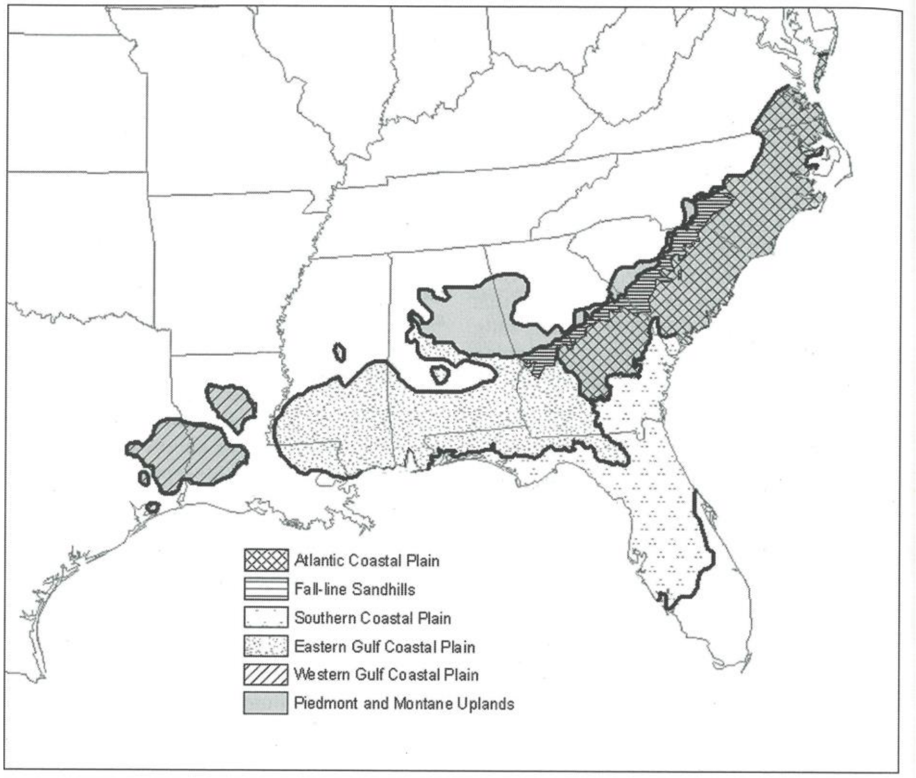


Figure 7. Six longleaf pine vegetation ecoregions, largely derived from EPA Ecoregions. From Peet 2006.

Table 1. Distribution of longleaf pine ecological groups by ecoregion. From Peet 2006.

Ecological Group	**Ecoregion**
Xeric Sand Barrens and Uplands	ACP, EGCP, FLS, SCP, WGCP
Subxeric Sandy Uplands	ACP, EGCP, FLS, SCP, WGCP
Silty Uplands	ACP, EGCP, FLS, WGCP
Clayey and Rocky Uplands	ACP, EGCP, FLS, PMU, WGCP
Flatwoods	ACP, EGCP, SCP
Savannas, Seeps and Prairies	ACP, EGCP, FLS, PMU, WGCP

ACP-Atlantic Coastal Plain, EGCP-East Gulf Coastal Plain, FLS-Fall-line Sandhills, PMU-Piedmont and Montane Uplands, SCP-Southern Coastal Plain, WGCP-West Gulf Coastal Plain.

Frequently burned sites with deep sandy soils support what are variously known as sandhill, high pine, or xeric sand communities. These communities are throughout the Southeast on alluvial sands, recently exposed terraces, relict dunes, and typic quartzipsamments of the Coastal Plain as well as along the fall line that marks the transition between Coastal Plain and Piedmont in the Carolinas and Georgia, and the southern Blue Ridge, Ridge and Valley and Cumberland Plateau region in northern Alabama and Georgia. Two distinct longleaf ecosystems occur on deep sandy soils: xeric and subxeric longleaf pine woodlands (Peet and Allard 1993, Christensen 2000). Xeric longleaf pine woodlands are characterized by widely scattered longleaf pines, a sparse to dense midstory of turkey (*Quercus laevis*) and bluejack oaks, and sparse to dense groundcovers dominated by wiregrasses (*Aristida stricta* north of the Congaree/Cooper rivers in South Carolina and *A. beyrichiana* to the south, Peet 1993). Within this xeric woodland type, 5 series have been identified (Peet and Allard 1993): fall line, Atlantic, and southern (Gulf) xeric longleaf woodlands, and Atlantic and Gulf maritime longleaf woodlands. Subxeric longleaf pine woodlands contain the above species as well as many more that are adapted to somewhat more moist conditions (Christensen 2000). This ecosystem type dominated much of the Coastal Plain uplands prior to European settlement (Ware et al. 1993, Christensen 2000). Peet and Allard (1993) identified 3 series within the subxeric ecosystem type: fall line, Atlantic, and Gulf subxeric longleaf pine woodlands.

Mesic and wet longleaf pine communities include flatwoods and savannahs, which differ from each other mainly in structure. Savannas are characterized by an open canopy and grass groundcover, whereas flatwoods have a somewhat denser canopy and a midstory of shrubs and subcanopy trees (Christensen 2000). The primary cause of variation between flatwoods and savannahs is interacting effects of fire and soil moisture (Peet and Allard 1993). Southern flatwoods include saw palmetto (*Serenoa repens*), gallberry-fetterbush (*Ilex glabra-Lyonia lucida*), and fern phases. If burned more frequently, these flatwoods may become more like savannahs (Christensen 2000). Longleaf pine savannahs contain many endemic species (Peet and Allard 1993, Walker 1993, Christensen 2000), and species diversity for these community types is among the highest in North America (Walker and Peet 1983).

Peet et al. (2018) geographically and coarsely characterized and mapped 8 broad regions of southern pine savannas based on dominance of tree and grass species (Figure 8), while describing how the complexity and diversity of longleaf pine communities is more appropriately categorized by the U.S. National Vegetation Classification (USNVC). The USNVC is a project by the U. S. Federal Geographic Data Committee (USFGDC 2008) to develop a nationally consistent, scientifically peer reviewed standard for the classification of natural vegetation types in coordination with NatureServe, federal agencies, Ecological Society of America, academia and other entities (USFGDC, Jennings et al. 2009). The USNVC consists of 8 hierarchical levels of classification. Upper levels delimit vegetation growth form, cover and structure. Lower levels circumscribe species composition and abundance. Middle levels reflect a combination of these criteria with ecological and geographic settings. The USNVC Longleaf Pine Woodland Macrogroup currently represents 4 Groups in which longleaf predominates with a total of 15 alliances and 119 associations (Table 2, U.S. National Vegetation Classification 2017, Peet et al. 2018).

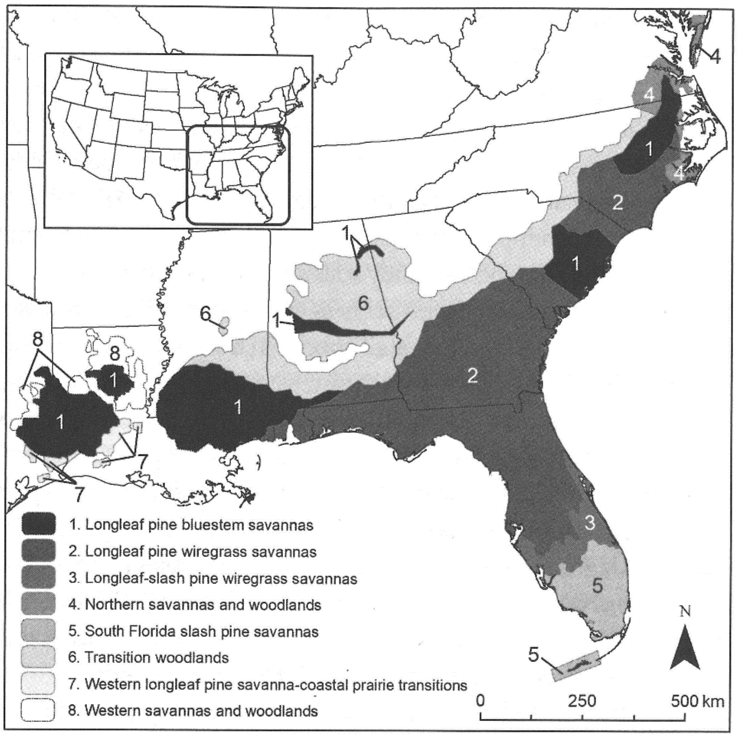


Figure 8. Range of six types of southern pine savannas based on abundance of overstory trees and ground-layer grasses. By Peet et al. 2018.

Table 2. Longleaf pine dominant groups with alliances and number of associations in the U.S. National Vegetation Classification.

Group	Alliance	Associations	States
Dry-Mesic Loamy LLP Woodland Group	WGCP LLP/Blackjack Oak/Bluestem Alliance	6	LA, TX
	WGCP Upland LLP/Bluestem Alliance	6	LA, TX
	Southeast CP LLP/Sand Post Oak/Wiregrass Alliance	6	NC, SC, GA, FL, AL, MS
	Southeast CP LLP/Blackjack Oak Clayhill Alliance	4	NC, SC, GA, FL, AL, MS
	Southeast CP Upland LLP/Wiregrass Alliance	14	NC, SC, GA, FL, AL, MS, LA
Xeric LLP Woodland Group	LLP/Bluejack Oak Sandhill Alliance	7	LA, TX
	LLP/Turkey Oak/Pineland Three-awn Alliance	9	VA, NC, SC
	LLP/Turkey Oak/Little Bluestem Alliance	9	SC, GA, FL
	LLP/Turkey Oak-Sand Live Oak Alliance	9	GA, FL, AL
	LLP/Turkey Oak/Three-awn Alliance	3	GA, FL, AL, MS
Wet-Mesic LLP Open Woodland Group	Atlantic Coastal Plain Wet LLP Savanna Alliance	14	NC, SC, GA, FL
	West Gulf Coastal Plain LLP Wet Savanna Alliance	3	LA, TX
	East Gulf Coastal Plain Wet Pine Open Alliance	8	GA, FL, AL, MS, LA
Mesic Longleaf Pine Flatwoods-Spodosol Woodland Group	Southern Coastal Plain Mesic LLP Flatwoods Alliance	16	SC, GA, FL, AL, MS, LA
	Atlantic Coastal Plain Mesic LLP Flatwoods Alliance	5	VA, NC, SC

The Xeric Longleaf Pine group, which includes subxeric soils, alliances and associations, occurs on mostly well-drained and excessively well-drained, deep coarse sands and sandy loams of the coastal plain and fall line Sandhills from North Carolina to Florida and west to eastern Texas. Physiognomically, this is probably one of the most distinctive and well-recognizes of the longleaf pine communities. The open woodland includes scrub oaks as turkey oak (*Quercus* *laevis*), bluejack oak (*Q. incana*) and sand post oak (*Q. margarettae*) east of the Mississippi River. Turkey oak is absent is absent west of the Mississippi River where it is replaced mostly by bluejack oak. The group spans the range of wiregrass (*Aristida stricta*) in North Carolina and northern South Carolina, southern wiregrass (*A. beyrichiana*) from southern South Carolina across much of Georgia, Florida to eastern Mississippi. Little bluestem (*Schizachrium scoparium*) is common throughout, although the herbaceous layer can be sparse on the most xeric sites.

The Dry-Mesic Loamy Longleaf Pine group consists of open upland stands on more fertile loamy sand or sandy loams from southeastern Virginia to east Texas, including most of Florida. The cover and development of the scrub oak component more characteristic of the Xeric Longleaf Pine group is absent. The West Gulf Coastal Plain Longleaf Pine/Blackjack Oak/Bluestem Woodland Alliance and West Gulf Coastal Plain Upland Longleaf Pine /Bluestem Woodland Alliance are major types, as indicated, west of the Mississippi River. Both types include associations with a well-developed and species rich herbaceous ground layer. East of the Mississippi River, the Southeastern Coastal Plain Longeaf Pine/Sand Post Oak/Wiregrass Woodland Alliance occurs in the Coastal Plain and Fall-line Sandhills, with or without wiregrass and southern wiregrass depending on the range, and with scrub oaks. The Southeastern Coastal Plain Longleaf Pine/Blackjack Oak Clayhill Woodland Alliance also occurs in the Coastal Plain and Fall-line Sandhills. This alliance includes associations in the loess loams of southwestern Mississippi, submesic types in the Tifton uplands of southern Georgia. The Southeastern Coastal Plain Upland Longleaf Pine/Wiregrass Woodland Alliance are open woodlands in the Coastal Plain and Fall-line with a herbaceous layer dominated by wiregrass, southern wiregrass or little bluestem, without a distinctive scrub oak component.

Figure 9. Mesic longleaf pine, Wade Tract, GA (left, photo credit Tall Timbers) and sandhill longleaf pine, Fort Bragg, NC (right).

The Mesic Longleaf Pine Flatwoods-Spodosol Woodland Group are open woodlands with 2 alliances with increasing soil moisture at flatwood sites from southeastern Virginia to east Texas with a grass-dominated herbaceous layer, and frequently with saw palmetto east of the Mississippi River in South Carolina, Georgia, and Florida. The Southern Coastal Plain Mesic Longleaf Pine Flatwoods Alliance is mostly in the outer Coastal Plain from South Carolina to Mississippi, including northern Florida. Shrubs on these mesic sites include gallberry (*Ilex glabra*) and bitter gallberry (*Ilex coriacea*) among a grass-dominated herb layer with southern wiregrass within its range and other species more characteristic of increasing mesic conditions as toothache grass (*Ctenium* aromaticum), bloodroot (*Lachnanthes caroliniana*), pineland daisy (*Chaptalia tomentosa*) and others. Slash pine and pond pine may be codominant with longleaf pine on wetter sites. The Atlantic Coastal Plain Mesic Longleaf Pine Flatwoods Alliance is a more northern alliance from southeastern Virginia to central South Carolina with wiregrass, creeping blueberry (*Vaccinium crassifolium*) and shrubs and forbs similar to the southern alliance. Pond pine may be codominant with longleaf pine on wetter sites.

The Wet-Mesic Longleaf Open Longleaf Pine Woodland Group is on poorly drained to somewhat poorly drained and seasonally saturated flats in the middle and and outer Coastal Plain from southern Virginia to east Texas. Wiregrass and southern wiregrass usually dominate within their geographic range, but toothache grass, cutover muhly (*Muhlenbergia expansa*), and other grasses may dominate or be codominant in the species rich herb layer that includes insectivorous plants. The Atlantic Coastal Plain Wet Longleaf Pine Savanna Alliance ranges in the Atlantic Coastal Plain from the Carolinas south to eastern Florida with a well-developed herbaceous layer. Toothache grass and shining fetterbush (*Lyonia lucida*) are characteristic elements. The highly diverse and variable herb layer of the open West Gulf Coastal Plain Longleaf Pine Wet Savanna Alliance of Louisiana and east Texas includes many grasses, forbs, and endemic species. The East Gulf Coastal Plain Wet Pine Open Woodland consists of mesic to wet savannas ranges from Florida and southern Georgia west to southeastern Louisiana, and sites in the Fall-line Sandhills of Georgia.

Figure 10. Longleaf pine flatwoods, Apalachicola National Forest, FL (left, photo credit Peet 2006), and longleaf pine-southern wiregrass savanna, Mississippi Sandhill Crane National Wildlife Refuge, MS (right, photo credit Oregon State University Forestry and Natural Resources Extension).

Figure 11. Dry-sandy longleaf pine, Angelina National Forest, TX (left) and dry-mesic longleaf pine, Kisatchie National Forest, LA (right, photo credits J. Van Kley).

These and other longleaf community types can support RCWs if sufficient old growth and mature pines are available for cavity trees and with adequate stocking in open forests for foraging. At sites of low productivity, extremely dry or wet locations, RCWs may need more foraging habitat than in mesic habitats because of small diameter pines and sparse densities (Hardesty et al. 1997, DeLotelle et al. 1987, 1995). These researchers have observed very large home ranges in some locations, possibly because arthropods are limited by sparse groundcovers or low pine density in areas of low site productivity. Expansion of home range size in these habitat types may also be a result of past alteration of the forest through overharvest or fire suppression: low site productivity can also affect how an ecosystem recovers following alteration (Provencher et al. 1997, 1998, 2001a). Whether the effect is natural or human-induced, some populations of RCWs in wet or very dry sites are using more foraging habitat.

Shortleaf Pine Communities

Shortleaf pine communities supporting RCWs occur in West Gulf Coastal Plain and Upper West Gulf Coastal Plain outside the natural longleaf pine range from the Ouachita Mountains of Arkansas and Oklahoma (McCurtain County Wilderness Area and Ouachita National Forest) and in eastern Texas (parts of Angelina National Forest, Davy Crockett National Forest, Sabine National Forest, Sam Houston National Forest, and the W. G. Jones and I. D. Fairchild State Forests). The western edge of the Cumberland Plateau in Kentucky (Daniel Boone National Forest) supported RCWs in shortleaf pine habitats until severely impacted by southern pine beetles in the summer of 2000 (Mills et al. 2004). Shortleaf pine communities are fire maintained, with a two-layered structure of pine overstory and diverse bunchgrass groundcover much like those of longleaf communities. Loblolly and other pines may be present as secondary components. Unlike most longleaf pine woodlands, many shortleaf pine communities supporting RCWs are in regions of complex topography (Masters et al. 1989, 1995, Kalisz and Boettcher 1991, Hines and Kalisz 1995, Zenitsky 1999). These rugged areas have steep and narrow ridges, with communities dominated by shortleaf pine confined to slopes of southern and western exposure and to the ridgetops (Masters et al. 1989, Foti and Glenn 1991, Kalisz and Boettcher 1991). Mesic sites such as drainages and north-facing slopes are typically dominated by white oak (*Quercus alba*) and some maples (*Acer* spp.; Masters et al. 1989, Foti and Glenn 1991). The shortleaf pine communities with RCWs generally correspond to open woodland associations with frequent fire in the USNVC West Gulf Coastal Plain Shortleaf Pine-Post Oak Forest Alliance.

Historic shortleaf pine/bunchgrass communities have sustained massive intrusion by hardwoods as a result of fire suppression and exclusion, and this intrusion caused precipitous declines of RCWs in these regions (Masters et al. 1989, 1995). Masters et al. (1995) estimated return intervals of fire in shortleaf pine ecosystems in rugged terrain prior to European settlement to be 3-6 years. Reintroduction of fire, using a prescribed burning program patterned after the precolonial fire regime, is vital to the survival and recovery of RCWs in these regions (Masters et al. 1989, 1995).

Figure 12. Shortleaf pine upland, McCurtain County Wilderness Area, OK (left, photo credit Oklahoma Department of Wildlife Conservation) and shortleaf pine-bluestem, Ouachita National Forest, AR (right, photo credit Larry Hedrick).

Loblolly Pine Habitats

Because of fire sensitivity, loblolly pine historically was much less widespread than today (White 1984, Landers 1991, Christensen 2000). Prior to fire suppression, loblolly pine was a minor component of riparian and other mesic forests in the Coastal Plain within the longleaf pine range and a secondary component of mixed pine and pine hardwood forests in interior uplands. However, loblolly pine is a significant natural component of forests, with shortleaf pine, west of the western range limit of longleaf pine in east Texas and north in Louisiana and Arkansas in the West Gulf Coastal Plain and Upper West Gulf Coastal Plain. Forests naturally dominated by loblolly pine and with RCWs today also are associated with nonriverine flatwood woodlands (e.g. USNVC-CEGL007069-West Gulf Coastal Plain Pine-Oak Nonriverine Flatwood Association) and related types in the West and Upper West Gulf Coastal Plain and, in northeastern North Carolina, nonriverine swamp and estuarine fringe woodlands (White 1984, Christensen 2000, Bragg 2002, Carter and Brust 2004, Smith et al. 2018b). For example, the RCW population in loblolly pine-hardwood at Felsenthal National Wildlife Refuge and Moro Big Pine (Bragg et al. 2014) in south-central Arkansas reflects general natural loblolly pine conditions. Currently, because of fire suppression during the past century and silvicultural practices favoring the species (White 1984), loblolly pine is the dominant pine throughout the Southeast in areas that were historically covered by longleaf pine, shortleaf pine, and shortleaf/loblolly pine forests (White 1984). These off-site loblolly pine forests have provided and continue to provide important resources for RCWs. However, ample opportunities exist for the careful restoration of site appropriate pines in areas currently dominated by off-site loblolly. The forests dominated by natural, historically occurring loblolly pine warrant special consideration and conservation. The foraging ecology of RCWs within natural loblolly pine habitat type has not been adequately studied.

Figure 13. Loblolly pine-hardwood, Felsenthal NWR, AR (left) and mature loblolly pine of natural origin at Moro Big Pine, AR (right, photo credit Don Bragg).

Pond Pine Communities

The remaining pond pine communities that support RCWs are found primarily in northeastern North Carolina (Smith et al. 2018b). Pond pine in this region was historically associated with pond pine savanna, woodland, canebrake and pocosin communities with natural fire return intervals from 2 to more than 20 years (Bailey et al. 2007). Today, pond pine woodland and pocosin with RCWs occur in a landscape matrix of other wetland communities, also with RCWs, including nonriverine swamp forest, estuarine fringe forest, and wet successional loblolly pine forest (Brust et al. 2004, Carter and Brust 2004, Dare County Bombing Range 2007). These pond pine and related wetland communities with RCWs, which usually are denser in the overstory and understory, are ecologically unique RCW habitats (Carter and Brust 2004, Smith et al. 2018b). Foraging resource preference, use, and requirements of RCWs in this habitat type have not been studied. Management of RCWs in pond pines and related wetland communities in this region, relative to other upland forest types, is complicated by the catastrophic nature of the natural and altered fire regime, dangerous accumulation of hazardous fuels during years of fire suppression, smoldering ground fire in organic soil, heavy smoke, limitations to the operation of heavy equipment on deep organic soils, southern pine beetle outbreaks, and high rates of cavity enlargement by pileated woodpeckers (J. H. Carter III, pers. comm.).

Figure 14. Pond pine woodland, Dare County Bombing Range, NC (left, photo credit J. H. Carter III & Associates) and pond pine high pocosin-woodland, Mattamuskeet National Wildlife Refuge, NC (right).

Slash Pine Communities

Slash pine communities dominated by the nominal slash (*P. elliottii* var. *elliottii*) are not considered to naturally widespread or significant types for RCWs. Slash pine is historically a minor component of coastal pine forests, although it can be naturally codominant with longleaf pine on wet sites. Slash is a mesic pine that was generally found in damp swales, narrow drainages, and along pond margins within longleaf pine forests (Landers 1991, Christensen 2000). Slash pine is now much more widespread than historically, as a result of fire suppression and aggressive planting programs to replace longleaf pine. Off-site slash pine forests support substantial numbers of RCWs in some areas as in Apalachicola National Forest. Restoration of slash pine sites to site-appropriate pines would be beneficial and is expected in the future.

In contrast, south Florida slash pine (*P. elliottii* var. *densa*) dominates natural communities in central peninsular Florida and southern peninsular Florida that support RCWs (Beever and Dryden 1992). South Florida slash pine is similar to longleaf in appearance, fire resistance, and possession of a grass stage and large taproot (Landers 1991). Much of the native slash pine used by RCWs is in hydric communities (Beever and Dryden 1992). It may be that slash pine replaces longleaf pine in this region because it can better tolerate very wet conditions.

Figure 15. South Florida slash pine at Jonathan Dickson State Park (left, photo credit Earl Leatherberry) and Big Cypress National Preserve (right, photo credit Mike Keys).

For RCWs, south Florida native slash pine habitats differ from slash pine habitats in that the pines are generally smaller and may be more sparsely distributed (Patterson and Robertson 1981, Beever and Dryden 1992, Landers and Boyer 1999). The largest size that south Florida slash pines achieve, even in old growth woodlands, is typically 20-30 cm (8 to 12 in) diameter at breast height (dbh). Cavity trees in this habitat type are much smaller than normally found in other habitats (Beever and Dryden 1992, Bowman and Huh 1995). However, the presence of fire and old trees in both nesting and foraging areas are critically important here as elsewhere.

RCWs inhabiting native slash pine habitat have not been well studied. Preliminary research has indicated that home ranges of birds in native slash pine are larger than those in other habitats (Patterson and Robertson 1981, Beever and Dryden 1992), but the relationship between home range size and habitat quality has not been investigated in this forest type. Larger home ranges in south Florida may result from degraded habitat, natural differences in habitat quality, population density, or even lack of cavity trees.

Tree Selection

Whether RCWs prefer to forage on a particular species of pine has not been clearly demonstrated, and it may be that no such preference exists. Previous research has yielded conflicting results, all of which could be confounded by other factors such as tree age and size, density of surrounding trees, and presence of hardwood midstory. Longleaf pines were selected over slash pines in northern Florida (Porter and Labisky 1986), but elsewhere in Florida slash pines were selected over longleaf (Nesbitt et al. 1978). Bowman et al. (1997) suggested that slash pine in south central Florida may provide important foraging in addition to longleaf. In the North Carolina Sandhills, RCWs did not select trees based on tree species, but over 90% of available pines were longleaf (Walters et al. 2000, 2002a). RCWs in coastal North Carolina did not select among longleaf, loblolly, and pond pines, even though the proportion of loblolly and pond pines together averaged over 20% of available pines (Zwicker and Walters 1999). It may be that in habitats that were traditionally longleaf, dominance of longleaf was sufficient to retard the evolution of selection among pine species by RCWs. Future research in habitat containing mixed pine species both historically and currently would help document the presence or absence of this behavior.

All studies examining selection of individual trees by foraging RCWs have found that the birds select large, old trees over small, young trees (Hooper and Lennartz 1981, Porter and Labisky 1986, DeLotelle et al. 1987, Bradshaw 1995, Jones and Hunt 1996, Engstrom and Sanders 1997, Hardesty et al. 1997, Zwicker and Walters 1999, Walters et al. 2000, 2002a). The general pattern for size selection is that RCWs select large pines and avoid small and medium-sized pines when sufficient large pines are available. Reported sizes below which trees are avoided (that is, used less than their availability) varies from 12.7 cm (5 in) dbh in coastal South Carolina (Hooper and Lennartz 1981), to 20.3 and 25.4 cm (8 and 10 in) dbh in northwest Florida (Porter and Labisky 1986, Hardesty et al. 1997) and Louisiana (Jones and Hunt 1996), to 25.4 cm (10 in) dbh in the North Carolina Coastal Plain and Sandhills (Zwicker and Walters 1999, Walters et al. 2000, 2002a). Reported sizes above which trees are selected (used more than their availability) include 20.3 and 25.4 cm (8 and 10 in) dbh in northwestern Florida (Porter and Labisky 1986, Hardesty et al. 1997), 25.4 cm (10 in) dbh in coastal South and North Carolina (Hooper and Lennartz 1981, Zwicker and Walters 1999), 30.5 cm (12 in) dbh in southwestern Georgia (Engstrom and Sanders 1997), the North Carolina Sandhills (Walters *et al.* 2000, 2002a), coastal Virginia (Bradshaw 1995), and Arkansas (Doster and James 1998), and 40 cm (15.7 in) in Louisiana (Jones and Hunt 1996).

Fewer studies have assessed specific ages at which individual pines are avoided or selected, although several more have assessed effects of average stand age (see below). Age and size of trees are highly correlated, at least until age 80 or greater (Platt et al. 1988b, Walters et al. 2000), and at present it is not known whether tree age, size, or both age and size is most important to foraging woodpeckers. In the Coastal Plain and Sandhills of North Carolina, trees under 60 years in age were avoided whereas those over 60 years (Coastal Plain) and 70 years (Sandhills) were selected (Zwicker and Walters 1999, Walters et al. 2000, 2002a). In northwestern Florida, trees less than 50 years in age were avoided, trees 50 to 150 years in age were used in proportion to their availability, and trees 150 years in age and older were preferred (Hardesty et al. 1997). The general pattern is similar to that for size selection: RCWs prefer older pines and make more use of younger trees when fewer older trees are available.

A preference by woodpeckers for the oldest and largest trees available has been shown in several studies (Hardesty et al. 1997, Engstrom and Sanders 1997, Zwicker and Walters 1999, Walters et al. 2000, 2002a). Bradshaw (1995) also reported a preference for the largest trees, although he combined all trees over 30.5 cm (12 in) dbh into one category. Such preference for the oldest and largest trees available suggests that tree selection by RCWs may be operating in either of two ways: (1) RCWs always select the oldest and largest trees in any habitat; or (2) an optimal size and age exists above which selection becomes equal, but this optimum remains unseen because currently these trees are not generally available in meaningful amounts (Zwicker and Walters 1999). There is evidence that selection tapers off for trees above age 60-70 years old, as well as a strong preference for old growth trees (Hardesty et al. 1997, Zwicker and Walters 1999). Thus, if an optimum exists, the age (and size) is older (and larger) than the trees generally available in the second-growth forests RCWs occupy.

Patch Selection

Habitat selection at a scale larger than individual trees, but smaller than stands, is referred to here as patch selection. Patch selection by RCWs has been explored in several studies. Bowman et al. (1997) found that RCWs foraged in patches containing fewer but larger trees than patches chosen randomly. Walters et al. (2000, 2002a) found that RCWs used patches containing larger trees with lower hardwood midstory than unused patches. Doster and James (1998) found that RCWs selected patches containing larger pines, a lower overstory pine density, and less hardwood midstory than randomly chosen patches nearby. According to the best predictive foraging patch selection model by Macey et al. (2016) in loblolly-shortleaf pines in east Texas, the hardwood midstory basal area was the most significant variable affecting patch use, where 95% of patches used were associated with midstory hardwoods of 0.98 m^2/ha (4.26 ft^2/acre). They also found a significant hardwood midstory basal area threshold of 0.36 m^2/ha (1.57 ft^2/acre) above which patch use declined.

Stand Selection

Use of stands by RCWs is influenced by the size of the stand, stand age, density of pines, density of large pines, fire history, hardwood midstory, season, and proximity to cavity trees and territorial boundaries (Hooper and Harlow 1986, Porter and Labisky 1986, DeLotelle et al. 1987, Epting et al. 1995, Bradshaw 1995, Walters et al. 2000, 2002a). Two studies documented a positive relationship between stand use and stand age after controlling for effects of cavity trees and territorial boundaries (DeLotelle et al. 1987, Epting et al. 1995). Porter and Labisky (1986) reported that preferred stands were much older than avoided stands (mean stand age = 72 and 18 years, respectively). Similarly, Jones (1994) reported that RCWs avoided stands of trees less than 50 years old, and that stand use increased continually with increasing stand age (Jones 1994, Jones and Hunt 1996). Hooper and Harlow (1986) also reported a weak positive effect of stand age on use.

Stand use and density of all pines may be positively related if densities are generally low (DeLotelle et al. 1987) and unrelated or negatively related if densities are high (Hooper and Harlow 1986, Bradshaw 1995). Effects of pine density on stand use also changes depending on the size of trees in question: increasing density of large trees is beneficial (Hooper and Harlow 1986, Bradshaw 1995, Walters et al. 2000, 2002a), whereas high densities of medium-sized and small pines are detrimental (Porter and Labisky 1986, Walters et al. 2000, 2002a). For example, stand use increased with increasing density of pines greater than or equal to 30.5 cm (12 in) dbh in Virginia (Bradshaw 1995), 35.6 cm (14 in) dbh in North Carolina Sandhills (Walters et al. 2000, 2002a), and 22.9, 35.6, and 48.3 cm (9, 14, and 19 in) dbh in coastal South Carolina (Hooper and Harlow 1986). Stand use decreased with increasing densities of pines less than 25.4 cm (10 in) dbh in North Carolina Sandhills (Walters et al. 2000, 2002a); similarly, RCWs avoided dense stands of young trees (average 559 stems/ac and 18 yrs in age) in northwest Florida (Porter and Labisky 1986).

Hardwoods have a negative influence on stand use. Stand use decreased with increasing density of hardwoods in several studies (Hooper and Harlow 1986, Epting et al. 1995, Bradshaw 1995, Jones and Hunt 1996), and stand use was negatively influenced by the average height of midstory hardwoods in North Carolina (Walters et al. 2000, 2002a). RCWs can tolerate some overstory hardwoods in foraging habitat. Inclusions of xeric hardwood species such as post, blackjack, and other oaks (*Quercus* spp.), especially in shortleaf pine forests, are natural components of the fire-maintained ecosystem (Kane et al. 2008, Hiers et al. 2014) and as natural inclusions do not need to be totally removed for woodpecker management (Service 2003). However, such hardwoods must remain a minor natural component overall in many habitat types, particularly longleaf: Jones and Hunt (1996) found that RCWs avoided stands in which greater than 10% of canopy trees were hardwoods. In contrast, canopy hardwoods may exist at higher densities in some habitats at the edge of the species' range. In the shortleaf forests of Oklahoma, precolonial density of hardwoods was an estimated 4.6 to 5.7 m^2 basal area per ha (20 to 25 ft^2/ac; Masters et al. 1995). Also in contrast to longleaf forests, there apparently is a greater hardwood component in shortleaf-loblolly and loblolly-shortleaf forests in east Texas, south-central Arkansas, and elsewhere in the Upper Coastal Plain north of the range of longleaf pine. The greatest hardwood densities are probably in unique RCW habitat in northeastern North Carolina wetlands (Carter and Brust 2004, Smith et al. 2018b).

Although habitat with a tall, dense midstory that resulted from fire suppression throughout much of the species' range clearly has negative effects on RCW foraging, and is avoided by RCWs, a modest hardwood midstory component is a natural feature of high quality foraging habitat.

Longleaf pine habitat without a legacy of fire exclusion maintained by frequent fire is characterized by scattered patches and trees of several small hardwoods, notably oaks.

Finally, during the non-breeding season RCWs may travel long distances to access open stands of large pines, whereas during the breeding season birds may use stands containing smaller pines or a greater hardwood component if they are near nest cavities (Bradshaw 1995, Jones and Hunt 1996).

Most of the research on foraging habitat selection described above had been conducted in longleaf and loblolly systems. Several studies indicate that foraging behavior of RCWs in shortleaf habitat is similar to that of RCWs in longleaf. RCWs foraging on shortleaf pines select large old trees in patches that have less hardwood midstory than the surrounding forest (Murphy 1982, Doster and James 1998, Zenitsky 1999). Similarly, the foraging ecology of RCWs in off-site loblolly is consistent with that of RCWs in predominantly longleaf forests: RCWs foraging on loblolly select older pines in open stands (e.g., Hooper and Harlow 1986, Zwicker and Walters 1999).

Home Range and Habitat Quality

Size of home ranges of RCWs have been described over much of the species' range and in several habitat types (Hooper et al. 1982, Wood 1983, Nesbitt et al. 1983, Repasky 1984, Porter and Labisky 1986, DeLotelle et al. 1987, Epting et al. 1995, Bradshaw 1995, Engstrom and Sanders 1997, Bowman et al. 1997, Hardesty et al. 1997, Doster and James 1998, Walters et al. 2000, 2002a). In studies with sample sizes of over 10 groups, estimates of average year-round home range size vary from 34 ha (84 ac) in southern Arkansas and northern Louisiana (Butler 2001), 43.1 ha (106.5 ha) in the upper coastal plain in Mississippi (Wood et al. 2008), 83.0 ha (205 ac) in the North Carolina Sandhills (Walters et al. 2000, 2002a), 87.0 ha (215 ac) in coastal South Carolina (Hooper et al. 1982), and 80.1 ha (198 ac) in coastal Georgia (Epting et al. 1995), to 108.9 ha (269 ac) on Eglin Air Force Base in the Florida panhandle (Hardesty et al. 1997) and 129.0 ha (319 ac) in central Florida (DeLotelle et al. 1995). Bradshaw (1995) reported that average year-round home range size for 6 groups in coastal Virginia at the northern edge of the range was 120.2 ha (297 ac), and Nesbitt et al. (1983) estimated that summer range for 5 groups in south Florida at the extreme southern edge of the range was 144.5 ha (357 ac). In the only study in old growth forest, Engstrom and Sanders (1997) reported that home range size for 7 groups in southwest Georgia was 46.9 ha (116 ac). Most RCW home ranges were estimated by the 100% minimum convex polygon (MCP) method and some by a 95% kernel density method (e.g., Worton 1989). MCP estimates typically are greater than the area utilization probability distribution estimated by kernel methods. Based on 95% kernel estimates, the smallest average annual home range size (n = 11 groups) was 28 ha (69 ac) (Butler 2001) and the largest (n = 12 groups) was 199 ha (492 ac) in peninsular Florida (Bowman et al. 2004).

Home ranges at the edges of the range, and especially in peninsular Florida, tend to be larger than those elsewhere, and those in fire-maintained old growth forest are substantially smaller than those in second-growth. This pattern suggests that the natural size and density of pines as well as degree of forest alteration (such as history of harvests and fire suppression) affects home range size. Variation of home range size within populations suggests a similar effect of habitat quality. Several studies have related variation in home range (or territory) size within a population to habitat characteristics of the home range (Hooper et al. 1982, Bowman et al. 1997, Hardesty et al. 1997, Walters et al. 2000, 2002a). Hooper et al. (1982) reported that for 24 groups in coastal South Carolina, territory size generally increased with increasing pine density and basal area. In contrast, Hardesty et al. (1997) reported that for 25 groups in northwest Florida, home range size decreased with increasing pine density and basal area. Walters et al. (2000, 2002a) found home range size of 30 groups in the North Carolina Sandhills was independent of pine density and basal area, but increased with increasing invasion by hardwoods. Thus, home range size depends on the quality of available foraging habitat: less habitat is required if the quality of that habitat is high. Increasing pine density may be beneficial if pine density is low or detrimental if density is high. This inverse relationship between quality and quantity of foraging habitat provides important evidence that foraging habitat can limit RCW population size for a managed property, and underscores the critical importance of restoration of foraging habitat to RCW conservation.

In summary, studies of home range size suggest that RCWs generally require from 40.5 to 161.9 ha (100 to 400 ac) per group, depending upon the quality of foraging habitat, and that high quality foraging habitat has an open structure with an intermediate pine density and sparse hardwood midstory. These characteristics of high-quality foraging habitat are consistent with those suggested by analyses of patch and stand selection (above) and group fitness (below). The research on home range sizes just described was conducted prior to widespread restoration of habitat and thus was based mostly on comparisons of fire-suppressed habitat to the limited amounts of fire-maintained habitat that existed at the time. These studies pointed to the limitation of RCW populations by the quality of their foraging habitat and illustrated the need for broad-scale habitat restoration.

In addition, the size of a home range or territory may increase if it is not constrained by the presence of neighboring groups (DeLotelle et al. 1987). Many RCW populations have increased greatly in size since earlier home range studies, and restored, fire-maintained habitat is much more prevalent now than it was then. Population densities in many locations are much higher now. Many managers report that budding and pioneering have produced extremely high local densities of RCW groups, invariably in areas of exceptionally high quality habitat and with suitable pines for natural cavity excavation. In the only comparative study of effects of RCW density on home range size, Garabedian et al. (2018) recently found that average home ranges

(95% kernel) and core defended areas (50% kernel isopleths) were larger at low densities (0.39 – 0.42 RCW groups/50 ha) than medium (0.57 – 0.60 groups/50 ha) and high (0.85 groups/50 ha) densities. Also, neighboring RCW group interactions and the overlap for home range and core areas was greater at high densities. In their study areas, Garabedian et al. (2018) concluded that with the establishment of minimally suitable baseline foraging habitat conditions, RCW group density and home range dynamics was determined more by the distribution of cavity trees. From these and other studies, it is not clear what the limits of territory size and population density of RCWs are in high quality habitat with an abundance of suitable pines for cavities. Therefore, it is quite likely that current carrying capacities for RCW populations are underestimated on properties managed to further enhance and increase habitat for foraging and cavity trees.

Group Fitness and Habitat Quality

Understanding the relationships between group fitness (e.g., reproductive success, group size, adult survival) and quantity and quality of foraging habitat is key to formulating appropriate foraging management guidelines for RCWs. To assess these relationships, other factors affecting group size must be considered. Two important factors are presence of helpers (Lennartz et al. 1987, Walters 1990, Neal *et al.* 1993a, Beyer *et al.* 1996) and increasing age and experience of breeders (Lennartz et al. 1987, Walters 1990, DeLotelle and Epting 1992), both of which are not only well documented, but well quantified (Heppell *et al.* 1994). Also, stochastic environmental events cause substantial variation in reproduction (e.g., Neal et al. 1993a; Letcher et al. 1998), and the large sizes of RCW territories make it challenging to directly measure foraging habitat use and quality in heterogenous forests at the territory level, limiting sample sizes. These sources of variation make it difficult to isolate the effect of habitat quality parameters in a multivariate environment. In their critical review of 11 multivariate studies on effects of foraging habitat to reproductive success, Garabedian et al. (2014) concluded that consistent and strong evidence was lacking to support many of the foraging habitat management criteria in the Service's 2003 RCW recovery plan, for which additional research was vitally needed.

Despite all these challenges, important progress has been made in determining effects of habitat quality on fitness. Most importantly, several studies have shown a positive relationship between fire frequency (as shown by groundcover) and fitness of RCWs (James et al. 1997, 2001, Hardesty et al. 1997). James et al. (2001) specifically documented an increase in fledging rate following the reintroduction of growing season fire relative to control plots burned during the dormant season. Frequent fire increases the quality of foraging habitat in several ways: it provides an open structure by reducing density of overstory and midstory pines and hardwoods, it encourages grass and forb groundcovers, and it may also increase nutrient cycling through the ecosystem and the nutrient content of prey (James et al. 1997). Numerous studies have documented direct correlations of RCW fitness with these habitat features. Group size and/or reproduction is negatively related to high pine density (Hardesty et al. 1997, James et al. 1997, 2001, Walters et al. 2000, 2002a) and extent of hardwood midstory (Walters et al. 2000, 2002a), and positively related to percent of wiregrass (*Aristida spp.*) or forbs in the ground cover (Hardesty et al. 1997, James et al. 1997).

Other studies have not found a relationship between group fitness and the size and age of canopy pines. The overall pattern is that fitness is positively related to the presence of old, large pines and negatively related to density of small and medium-size pines. In the North Carolina Sandhills, group size was negatively related to density of pines less than 35 cm dbh (14 in; Walters *et al.* 2000, 2002a). In Louisiana, density of groups, group fitness, and the number of old growth trees (90 to 120 years in age) were all strongly positively related (Conner et al. 1999). In Texas, group size increased with increasing area of pines greater or equal to 60 years in age both within 400 meters of the cluster (Conner and Rudolph 1991b) and at a larger, regional scale (520 to 5200 ha, Rudolph and Conner 1994). Similarly, in the North Carolina Sandhills, group size increased with increasing density of flattops (very old pines) (Walters et al. 2000, 2002a).

A recent, rangewide study of populations on 5 Department of Defense installations confirmed that relationships of group fitness (e.g., group size and fledgling production) to these same habitat features persist in the improved conditions characterizing today's habitat, as well as providing new insights that apply to restored, fire-maintained habitat conditions (McKellar et al. 2014). Greater basal area and numbers of large pines (>35 cm dbh, 14 in dbh) and a greater herbaceous groundcover component had the largest and most consistent effects and were associated with higher group fitness. Threshold effects were evident for both features. Results suggested the optimal density of large pines may be above the level specified in the Recovery Plan (USFWS 2003), but that there is also an upper limit to large pine density, above which negative impacts occur (estimated at 9.2 m^2/ha [40 ft^2/acre] basal area and 90 stems/ha [36 stems/ac]). This upper threshold likely is mediated by reduction of herbaceous groundcover due to shading effects (Hiers et al. 2007). An upper limit to benefits of a greater herbaceous component in the groundcover was evident, and the 40% figure adopted in the Recovery Plan (USFWS 2003) appears to be an appropriate value for this threshold, although the threshold may be higher at some locations (McKellar et al. 2014). In a separate study at the Savannah River Site in South Carolina (Garabedian et al. 2017), fledgling production was significantly and negatively affected by number of pines ≥ 35.6 cm dbh/ha and positively affected by group size in the best multivariate upper piecewise linear regression model of foraging habitat resource utilization.

Although the positive effects of large pines and herbaceous cover to fitness are evident on current landscapes, negative effects of hardwood midstory are not (McKellar et al. 2014). It appears that the extent of hardwood midstory is below the threshold at which this effect occurs in most, but not all (e.g., Fort Jackson) locations, where RCW habitat is effectively restored and managed. Results suggest that a modest hardwood component, in contrast to a dense hardwood midstory layer, does not produce negative fitness impacts. However, evidence indicates RCW foraging habitat resource use at some sites continues to be sensitive to hardwood midstory conditions. RCW foraging patch use declined significantly with > 0.4 m^2/ha (1.7 ft^2/acre) of small hardwoods at a South Carolina site (Garabedian et al. 2017) and > 0.36 m^2/ha (1.57 ft^2/acre) in east Texas (Macey et al. 2016). Effective management to restore and control fire-intolerant midstory hardwoods remains important to support sufficient foraging resources and fitness levels.

Of course quantity, as well as quality, of foraging habitat may affect group fitness. Territory or home range size has been shown to affect group size and/or reproduction in some populations (USFWS 1985, DeLotelle and Epting 1992, Hardesty et al. 1997, Convery 2002) but not in others (James et al. 1997, Walters et al. 2000, 2002a). For 2 studies reporting an influence of home range/territory size on fledgling production, much of the effect appears to have come from nest loss or failure to nest (DeLotelle and Epting 1992, Hardesty et al. 1997). Home range size for successful and unsuccessful nesting groups in northwest Florida averaged 126.3 and 72.4 ha (312 and 179 ac) respectively (Hardesty et al. 1997). This suggests that there is a threshold home range size below which density-dependence affects reproduction. Recent studies of high local densities support this conclusion (Garabedian et al. 2018). Densities in high quality, restored habitat, as well those observed in the few old growth longleaf forest remaining, may indicate the threshold at which density-dependence effects occur. Home ranges in the fire-maintained, old growth longleaf forest of the Wade Tract in Georgia averaged only 46.9 ha (116 ac) (including considerable overlap among home ranges, Engstrom and Sanders 1997). These groups have among the smallest average home range sizes and highest group sizes and productivity yet reported (average group size 3.0 to 3.6; average fledglings from successful nests 2.3 to 2.5; Engstrom and Sanders 1997), suggesting that the density at which density-dependence effects are manifested may be even lower in fire-maintained, old growth habitat.

In conclusion, the fitness of RCW groups increases if groups have substantial amounts of foraging areas that are burned regularly such that they have sparse hardwood midstory and an abundant grass and forb groundcover, as well as low densities of small and medium-sized pines and high densities of large, old pines. These observed relationships between foraging habitat characteristics and RCW fitness are consistent with those from studies of tree selection, patch selection, stand selection, and home range/habitat quality relationships. This suggests that the correlations observed reflect causal relationships.

Population Structure

Given the historic distribution of its habitat and comments by early naturalists about its abundance, it is highly likely that RCWs originally were distributed continuously over broad areas (Conner et al. 2001a). Since the birds are so sedentary, one presumes that originally there may have been considerable genetic substructure within populations, but that distinct, genetic population boundaries were lacking. That is, genetic similarity probably changed gradually with distance, rather than suddenly at population boundaries. In fact, it likely was difficult to delineate distinct populations.

RCWs are currently distributed largely as distinct populations with large gaps of unoccupied land between them. Most of these populations are quite small, and only a few are of more than modest size. Typical dispersal distances of both sexes are sufficiently short to maintain genetic substructure within populations even under current conditions. Daniels and Walters (2000a) found that an individual's close relatives are highly concentrated within 3 territories of the individual's natal site. Thus, one can expect genetic similarity to change with distance within populations, as opposed to the uniform structure that occurs when mating is random within populations.

The RCW is highly sedentary compared to most other birds. Adult helper males disperse the shortest distance to nearby territories, as in the North Carolina Sandhills (median 1.27 km, 0.79 mi) (Kesler et al. 2010). Juveniles exhibit 2 dispersal behaviors following prospecting forays from their natal territory (Pasinelli and Walters 2002, Kesler et al. 2010). In the prevailing short-distance mode, juvenile males and females moved a median, respectively, of 2.94 km (1.83 mi) and 3.31 km (2.06 mi) in the Sandhills (Kesler et al. 2010). Following extraterritorial forays at much greater distances than their normal forays, some juveniles engaged a less frequent jumper behavior to acquire positions at other territories at a mean distance of 9.9 km (6.15 mi) from their natal territory (Kesler et al. 2010).

At greater distances, rare long distance RCW dispersals of 27 – 325 km (17 – 202 miles) between populations are known from some banded individuals in monitored populations (Walters et al. 1988b, Conner et al. 1997c, Ferral et al. 1997, Lowery and Perkins 2002, Costa and DeLotelle 2006). Because the number of banded RCWs monitored for individual identification is small relative to the total number of RCWs, there is sufficient documentation to conclude that long-distance movements between populations are rare but likely regular events. It appears that movement occurs from small to large populations and vice versa (Walters et al. 1988b, Costa and DeLotelle 2006). Because of this, and the rarity of such movements, they are of little consequence demographically; that is, their contribution to sustaining populations is trivial. However, they may be frequent enough to be important genetically, and may function to maintain genetic variability within populations. Thus, RCW populations should not be viewed as closed genetically. Producing immigrants that contribute to movement between populations may be one of the primary purposes that small support populations serve. However, rates of immigration and genetic relationships between populations, and effects of landscape forest fragmentation and habitat conditions on suitable connectivity for genetically effective long distance dispersals are not well enough known to determine precisely the rate of gene flow, nor its effect on genetic variability within populations.

The most reasonable conclusion, based on current information, is that demographically, populations of RCWs as we define them (see below) function as closed populations. That is, their persistence depends totally on within-population demography and not on exchange between populations. Thus, RCWs do not exhibit any of the various types of classic metapopulation structure (Stith et al. 1996). Local extinction followed by natural recolonization from another population is extraordinarily unlikely for this species due to their dependence on already existing cavities. The event closest to natural recolonization was the appearance of a male from the Savannah River Site within a recruitment cluster on Fort Gordon 2 years after the Fort Gordon population was extirpated. Still, this dispersal event may not have occurred in the absence of artificial cavities, and likely would not have resulted in the formation of a breeding pair without subsequent translocation of additional birds into the population.

Further, immigration rates are too low for one population to rescue another from extinction as occurs in another cooperatively breeding woodpecker, the acorn woodpecker (*M. formicivorous*; Stacey and Taper 1992). Neither are immigration rates high enough to enable source-sink relationships between populations. However, in areas of low density (e.g., northeastern North Carolina, south Florida), widely scattered groups considerable distances apart separated by habitat conducive to dispersal may function as a single population (e.g., Costa and DeLotelle 2006). RCWs appear to be willing to move through forested habitats not suitable for occupancy, such as pocosin, during long distance dispersal. Dispersal distances are longer when population density is lower (Daniels 1997, Kesler et al. 2010), apparently because the distance moved is a function primarily of the number of groups encountered rather than of habitat, mortality or speed of movement. Thus migration between 2 sizeable populations only 24.2 km (15 mi) apart may be rare (e.g., only one movement between the Camp Lejeune and Croatan National Forest populations in North Carolina over 11 years), whereas 2 groups 24.2 km (15 mi) apart in an area of low density (e.g., only one other group between them) may exchange individuals regularly.

There are both allozyme (Stangel et al. 1992, Stangel and Dixon 1995) and random amplified polymorphic DNA (RAPD) data (Haig et al. 1994a, 1996) available that reveal general genetic relationships between populations. These data indicate that most (93%, Haig et al. 1994a) genetic variation occurs among individuals within populations, rather than between populations. Genetic differences between populations increase somewhat with geographic distance, but there is little geographic structure to genetic variability. Genetic differences between populations are greater than is typical of birds, but equivalent to those in other endangered birds. However, populations do not exhibit unique alleles. Some small populations exhibit reduced heterozygosity, but not all do, and generally there is no consistent relationship between population size and genetic variability (Stangel and Dixon 1995). All of this information is consistent with recent isolation of populations in a formerly continuously distributed species, with low levels of gene flow between populations. Populations probably are diverging genetically and losing variability currently, but isolation evidently is too recent for them to differ much yet.

Population Dynamics

The population dynamics of the RCW are intimately related to the species' unusual social system (Walters 1990, 1991). In demographic terms, the presence of a large class of nonbreeding adults, helpers, strongly affects population dynamics. Helpers provide a pool of replacement breeders in addition to young of the year, and thereby act as a buffer between mortality and productivity in regulating population size. That is, the number of breeding groups in one year is not strongly affected by either productivity or mortality in the previous year. Instead, the size of the helper class is affected by these variables, while the number of potential breeding groups remains remarkably constant. If mortality exceeds productivity, the number of helpers will decrease, because the number of replacement breeders drawn from the helper class will exceed the number of fledglings recruited into it. If productivity exceeds mortality, the opposite will occur, and the number of helpers will increase. Therefore, average group size is an important indicator of population condition as it indicates the potential to maintain the size of the breeding population in the face of fluctuations in mortality and productivity. Of course, the strength of the buffering effect of helpers depends on the size of the helper class. In small populations, the number of helpers may be so few that poor survival or reproduction can have a direct, negative effect on the size of the breeding population (Lennartz and Heckel 1987, DeLotelle et al. 1995).

In evolutionary terms, adoption of the helping strategy is closely linked to patterns of territory occupancy (Walters 1990, 1991). Remaining on the natal territory as a helper can be viewed as a strategy involving delayed reproduction and dispersal, and altered dispersal behavior, to acquire a breeding position. Helpers stay at home and wait for a breeding vacancy to arise in their vicinity, either on the natal territory or a neighboring one (Walters et al. 1992b). This strategy is effective when competition for breeding vacancies is intense (Zack and Rabenold 1989). Further, the intense competition for breeding vacancies that characterizes cooperative breeders is thought to result from unusually large variation in territory quality (Stacey and Ligon 1991, Emlen 1991, Koenig et al. 1992).

In RCWs, variation in territory quality is related to the presence of cavities. Because cavities take so long to construct, an individual does better if it acquires a breeding position on an existing territory containing suitable cavities than if it occupies vacant habitat and must construct new cavities (Walters 1991, Walters et al. 1992a, Conner and Rudolph 1995a). Thus, habitat lacking suitable cavities is poor quality, and habitat with existing, suitable cavities is high quality. The birds ignore poor quality habitat, even though they could excavate cavities and then reproduce successfully there, and compete intensely for openings in high quality habitat. When artificial cavities are added to unoccupied but otherwise suitable habitat, it immediately becomes high quality habitat, and is quickly occupied (Copeyon et al. 1991, Walters et al. 1992a).

The implication of this view of population dynamics is that the number of high quality territories, which depends on the number and distribution of suitable cavities, determines breeding population size (usually measured as the number of potential breeding groups). This is consistent with the behavior of populations during the species' decline, as well as with recent increases under new management that employs recruitment clusters to increase the number of occupied territories and cavity management to maintain occupancy of existing territories (Walters 1991). The dominant feature in population declines has been gradual abandonment of territories rather than poor survival or reproduction. In many cases, it is clear that territory abandonment was related to loss of cavities to tree death or cavity enlargement, or to encroachment by hardwood midstory (Jackson 1978b, Van Balen and Doerr 1978, Conner and Rudolph 1989, Costa and Escano 1989). With so many threats to cavities, it was easy to lose territories, and thus populations declined, despite the continued presence of helpers and good productivity on those territories that remained suitable. During population declines, territories often were occupied by an unpaired male for a period prior to abandonment, so that response to loss of cavities and other adverse events was delayed (Jackson 1994). This may be because once territories deteriorate, young birds no longer remain as helpers and females no longer consider them acceptable, but the breeding male refuses to leave. The territory is no longer acceptable to dispersing males, however, so once the original breeding male dies, which may be many years later, the territory is finally abandoned.

New groups on new territories arise by 2 processes, pioneering and budding (Hooper 1983). Pioneering is the occupation of vacant habitat by construction of a new cavity tree cluster, which, in accordance with the view of population dynamics just presented, should be rare. Budding is the splitting of a territory, and the cavity tree cluster within it, into 2 clusters occupied by separate groups. Budding is common in many other cooperative breeders, and should be more common than pioneering in RCWs (Walters 2004), as the new territory contains cavities from the outset. The available data indicate that budding indeed is more common than pioneering, and that pioneering is quite rare. In the North Carolina Sandhills, the observed rate of pioneering over 16 years was one event per 1572 existing groups per year, and in Croatan National Forest in coastal North Carolina, over 7 years it was one event per 332 existing groups per year (J. Walters, unpublished). These translate into rates of new territory formation (relative to the current population size) of 0.06% and 0.3% per year. However, at nearby Marine Corps Base Camp Lejeune, the rate of pioneering over 10 years was one event per 46 existing groups per year, a rate of new territory formation of 1.5% per year (Walters 2004). During these same periods, rates of territory increase through budding were 0.6%, 2.1%, and 0.6% for the North Carolina Sandhills, Croatan National Forest, and Marine Corps Base Camp Lejeune respectively.

Combining budding and pioneering, rates of territory increase were 0.7%, 2.4%, and 2.2% per year respectively. During a period when the North Carolina Sandhills population was declining (1980 to 1984) the rate of territory increase through these processes was 0.1% per year, whereas over the subsequent years, when the population was stable, it was 0.9%.

The causes of variation in rates of budding and pioneering are not entirely clear. One hypothesis is that rates are higher where turnover of breeders is less, and thus opportunities to replace deceased breeders are fewer. It is indeed young males (age 1-3), whose prospects for obtaining breeding positions are lower than those of older males, who are responsible for the preponderance of budding and pioneering events (Perkins 2006). Also, this hypothesis is consistent with observations of an inverse relationship between rates of budding and pioneering and availability of recruitment clusters (Walters 2004). It may also be that improvement in territory quality through habitat restoration and an increasing availability of older pine for natural cavity excavation stimulates budding and pioneering. This second hypothesis is consistent with increases in rates of budding and pioneering in recent years, and particularly with the development of areas of extremely high densities of RCWs mentioned above, which in all cases arose through multiple instances of budding and pioneering rather than being stimulated by creation of recruitment clusters. Even under these conditions, however, rates of budding and pioneering remain quite low. These rates were too low to counter losses of territories during the 1970s and 1980s when populations were declining, and they limit the rate at which populations can recover, even if losses of territories can be prevented. The high rates of population growth that have occurred in many locations since the late 1990s in all cases have been driven by artificial cavity construction, that is, the creation of new territories through recruitment cluster construction (see below), not budding and pioneering.

Understanding that population size is determined by the number of territories with suitable cavities makes designing management to increase populations straightforward (Copeyon et al. 1991, Walters 1991). To prevent loss of occupied territories, existing cavity trees should be protected, so that a sufficient number of suitable ones are maintained at all times. This can involve eliminating encroaching hardwoods, protecting cavities with restrictors (Carter et al. 1989), or replacing lost cavities with artificial ones. To increase the number of suitable territories, cavities can be added in unoccupied habitat, such as abandoned territories with existing cavities and completely vacant areas. In theory, it might be possible to rehabilitate abandoned territories by placing restrictors on existing cavities or eliminating hardwoods. In practice, however, only recently abandoned territories seem to be reoccupied without the addition of new cavities (Doerr et al. 1989, Saenz et al. 2001). This may be because cavities deteriorate if unused for long periods. Therefore, for both abandoned territories and vacant habitat, usually the only effective means to create a suitable territory is to construct new artificial cavities.

A management strategy based on maintaining and creating suitable territories using artificial cavities, coupled with restoration and maintenance of habitat through prescribed fire and other treatments, and translocation to augment populations of fewer than 30 groups developed in the 1990s (Walters 1991, Rudolph et al. 2004) and codified in the second revision of the RCW Recovery Plan (USFWS 2003) has been widely applied with great success. The rates of population growth presented in Chapter 4 document this success. Rates of population increase are similar across sites, suggesting that a rate of increase of 5 - 10% per year is perhaps the best that can be achieved without resorting to translocation. It may be that the pool of potential new breeders (i.e., helpers, floaters, and first-year birds) generally is not large enough to permit higher rates of increase.

The current understanding of population dynamics suggests that management designed to increase the number of suitable territories will be effective, while management designed instead to increase productivity and survival will be ineffective to increase populations in most circumstances. Thus, measures designed to thwart nest predators, prevent cavity kleptoparasitism (except to prevent cavity enlargement), or eliminate predators of fledglings and adults often will be ineffective in promoting population growth (Walters 1991). Such measures may be necessary, however, in intensively managed, small populations where every individual is critically important.

Population Models

Demographic stochasticity refers to effects of random events on the reproduction and survival of individuals, whereas environmental stochasticity refers to effects of unpredictable but nonrandom events that alter vital rates. For example, if every individual has a 50% probability of annual survival, in a population of 20 individuals one does not expect exactly 10 to die each year. Instead some years by chance 9 will die, in others 11 and so forth. This is demographic stochasticity, which is analogous to sampling error. It may be that in years with severe winters the probability of survival is only 30%, whereas in years with mild winters it is 70%. This is an example of environmental stochasticity.

Demographic stochasticity is inevitable, but is usually considered to be a threat only to small populations, i.e., those with less than 50 individuals (Meffe and Carroll 1997). Environmental stochasticity often takes the form of annual variation, and varies widely in strength, depending on the species and the nature of its interactions with its environment. The available data indicate that in RCWs, annual variation in productivity is considerable, whereas annual variation in mortality is fairly small (Walters et al. 1988a). Viability in the face of these threats usually is assessed by incorporating them in model simulations of population dynamics, and determining the probability of extinction over long time periods in populations of various sizes. The complex social system of the RCWs poses a challenge for modeling the species' population dynamics.

Standard, simple population models do not incorporate the social complexity of the species, notably the buffering effect of the potentially large, nonbreeding helper class. The buffering effect can be handled to some extent by stage-based matrix models (Caswell 1989, McDonald and Caswell 1992). Application of these models to RCWs has produced important insights about population behavior and management (Heppell et al. 1994, Maguire et al. 1995). However, even these models do not incorporate critically important spatial dynamics resulting from helpers filling breeding vacancies only on or very near their natal territory. A model that assumes that nonbreeders fill breeding vacancies randomly within the population cannot be expected to portray population dynamics accurately enough to perform viability analysis.

The advent of spatially-explicit, individual-based simulation models in ecology provided a tool capable of handling the complex population dynamics of RCWs (DeAngelis and Gross 1992, Judson 1994, Dunning et al. 1995). These models are not without their faults, a notable one being the large number of parameters that must be accurately estimated if model results are to be robust (Conroy et al. 1995). A spatially-explicit, individual-based model (SEPM) of the population dynamics of RCWs was developed by Letcher et al. (1998) using data from the North Carolina Sandhills. Later versions of the SEPM incorporated both demographic and environmental stochasticity (Walters et al. 2002b) and was validated with actual population data from the Sandhills and North Carolina Coastal Plain (Schiegg et al. 2005). In comparison to earlier RCW population models, the RCW SEPM (e.g., Walters et al. 2011) with spatial and social dynamics more accurately simulated actual RCW populations (Zeigler and Walters 2014). Various applications of the RCW SEPM (Letcher et al. 1998, Crowder et al. 1998, Walters et al. 2002b) demonstrated the strong effect of spatial structure on viability arising from territory density and the limited dispersal range of helpers and juveniles. In these simulations habitat was assumed to be limited, and formation of new territories was limited to budding and pioneering. Modeling results suggest that populations of 100 or fewer groups are vulnerable to extinction, even when territories are maximally clumped. However, populations of as few as 25 groups may be remarkably persistent, albeit still declining. The model predicts that populations of 250 groups or more would always be stable regardless of the distribution and density of territories, a testament to the stabilizing influence of the buffering effect of helpers. These model results are consistent with empirical evidence. Across the range it is evident that small aggregates of groups persist surprisingly well with effective management to avoid cavity and habitat limitations, whereas small, low density populations always seem to decline. Even in somewhat larger populations, loss of isolated groups is a problem (Conner and Rudolph 1991b).

The Recovery Plan (USFWS 2003) concluded that demographic stochasticity is, as usual, a threat only to small populations. However, the threshold of vulnerability varies considerably with spatial structure. Vulnerable populations may be twice the typical size, or half the typical size, depending on the density and configuration of the population. It certainly is possible to avoid this threat for populations as small as 25 groups, and it may be possible to avoid it for populations of only 10 groups with intensive management. Managers therefore should strive to aggregate their populations, and to avoid isolation of groups, where isolation is defined as being beyond the dispersal range of helpers. Based on data from North Carolina (Walters et al. 1988a, Kesler et al. 2010), 3 km (1.9 mi) is a reasonable standard to use for the maximum dispersal range of helpers (less than 10% of helpers [17 of 240] dispersed more than 3.2 km [2 mi]; Daniels 1997). This maximum dispersal distance refers to habitat that contains no barriers to dispersal. The ideal spatial configuration is one in which every group is within dispersal range of helpers from several other groups.

These modeling studies suggest the population sizes necessary to achieve viability in the face of demographic and environmental stochasticity are much smaller than is typical for bird species. This is an intuitive result since the presence of helpers can be expected to dampen oscillations in the breeding population caused by variation in productivity and breeder survival. Years of poor productivity, or low breeder survival, will lead to a reduction in the size of the helper class rather than a reduced number of potential breeding groups. These studies also suggest that the level of assistance, in the form of translocated birds, required to avoid extinction of small populations may be low enough to be feasible. Finally, they clearly demonstrate that spatial configuration of territories becomes increasingly important to viability as populations become smaller.

Genetic Considerations

There are 2 genetic threats to population viability. The first, inbreeding depression, threatens only small populations, whereas the second, genetic drift, can threaten even large populations (reviewed in Lande 1995). Inbreeding depression reduces the survival and productivity of individuals, and results from the segregation of partially recessive, deleterious alleles. The resulting negative effect on population dynamics increases vulnerability to extinction. The amount of inbreeding depression depends on the rate of inbreeding and the opportunity for selection to purge recessive lethal and semi-lethal mutations (Lande 1995). Genetic drift results in the loss of genetic variation, which may reduce a species' ability to adapt and persist in a changing environment, and thereby its viability over long time periods. The rate of loss is inversely related to population size and mutation rate, and viability is achieved when the population size is large enough that loss to drift is in equilibrium with gain from mutation.

Inbreeding in RCWs is avoided or reduced by several mechanisms. Breeding females typically disperse if their son, as a subadult or helper, inherits the breeding male position on their territory (Walters et al. 1988, Daniels and Walters 2000b). Also, subadult females usually disperse from their natal territory, instead of acquiring a vacant breeding position, if the breeding male is closely related (e.g., father or sibling) (Daniels and Walters 2000a). However, dispersing females encounter and breed with related males on nearby territories due to their relatively short natal dispersal distances (Daniels and Walters 2002a) that increases the risk of inbreeding depression (Walters et al. 2004, Schiegg et al. 2006). Young females can recognize kin on their natal territory, but not necessarily close relatives on neighboring territories (Daniels and Walters 2000a).

The RCW is one of the few species for which inbreeding depression has been demonstrated in wild populations, as opposed to assumed from theoretical considerations. In the North Carolina Sandhills, productivity of both closely related (i.e., coefficient of relationship greater than 0.125) pairs and their inbred progeny is substantially lower than that of unrelated pairs and their progeny (Daniels and Walters 2000a). This is due to both reduced hatching rates of eggs and reduced survival of fledglings to age one year. Although inbreeding depression was demonstrated for certain RCW groups in the NC Sandhills, it was not manifested throughout this large population that has increased substantially with active conservation management. Inbreeding depression with high rates of hatching failure also has been detected as a population-level phenomenon at the small (e.g., < 30 active clusters) Avon Park Air Force Range population in south Florida (Schrott et al. 2010, Aldredge et al. 2016). These are precisely the sort of traits one expects to be affected by segregation of partially recessive, deleterious alleles, and in fact reduced hatching rate is the classical manifestation of inbreeding depression in domestic birds (Daniels and Walters 2000a).

Immigration is critical to mitigate adverse effects of inbreeding depression that can further increase the likelihood of decline and extirpation in small populations. Schiegg et al. (2006) used the RCW spatially explicit model (Walters et al. 2002b) with empirical inbreeding depression data to find that the risk of extirpation in highly aggregated initial populations of 25, 49 and 100 territories without immigration was significantly greater with inbreeding depression. Even for relatively large and aggregated initial populations of 100 breeding groups, 78% were extirpated within 100 years with inbreeding depression compared to 2% without inbreeding effects (Schiegg et al. 2006). Daniels et al. (2000), using the spatially explicit individual-based model developed by Letcher *et al.* (1998), estimated inbreeding levels over time in RCW populations of various sizes and rates of immigration. In their simulations, mean inbreeding increased rapidly in very small, declining populations with no immigration, but remained tolerably low in closed, stable populations of 100 occupied territories. Moderately high levels of immigration were required to stabilize small declining populations and maintain reasonable inbreeding levels (kinship coefficients less than 0.10). That is, inbreeding depression is not expected to affect populations that are receiving 2 or more migrants per year.

The rare long distance RCW dispersals documented between some populations (e.g., Costa and DeLotelle 2006) are insufficient to determine if the frequency of immigration is adequate to offset risks and adverse effects of inbreeding depression for most RCW populations. In the North Carolina Sandhills, Trainor et al. (2013) found that most juvenile females prospecting for new territories and during dispersal from natal territories tended to move 1 – 6 km (0.6 – 3.7 mi) through habitat similar to that for foraging, but not at longer distances. RCW long-distance dispersal behavior is probably different and less sensitive to a heterogeneous matrix of landscape forest and non-forest conditions, but additional research is required to identify suitable landscape conditions that connect fragmented RCW populations with effective long distance dispersal (Trainor et al. 2013).

Without reliable direct data on RCW immigration rates, genetic data can provide an indirect, although coarse, estimate of immigration rates. Haig et al. (1996) estimated gene flow (N_m) as 1.26 migrants per generation among 6 populations in south Florida and 0.95 migrants among 20 rangewide populations based on random amplified polymorphic DNA (RAPD) and Wright's (1951) island population genetic model [$N_m = 0.25(1/F_{st} – 1)$]. An average RCW generation is about 4 years (Reed et al. 1988b). These migration rates per generation are inadequate to deter inbreeding depression in small RCW populations according to the annual rates of at least 2 or more estimated by Daniels et al. (2000) from spatially explicit individual-based models, pedigree analysis and empirical inbreeding depression data. Absolute migration rates estimated by these genetic methods should be interpreted cautiously because of a number of assumptions required for the island population genetic model that likely are unrealistic for actual RCW populations (e.g. Whitlock and McCauley 1999).

Although inbreeding depression is clearly a threat to RCW populations, its effects may not yet be evident due to the relatively recent nature of fragmentation and reductions in population size. The available genetic data with RAPD indicate that most small populations do not yet exhibit high levels of homozygosity (Haig et al. 1994a, 1996). Furthermore, Stangel and Dixon (1995) found no evidence that small populations were experiencing increased morphological variability. They examined fluctuating asymmetries of paired characters, which are often used as an indicator of developmental stability (Leary and Allendorf 1989). Developmental instabilities are thought to be one of the manifestations of inbreeding depression.

Inbreeding is expected to increase in populations that remain small and isolated. Franklin (1980) suggested that populations with an effective size of 50 individuals or less would be vulnerable to inbreeding effects. Since the RCW can be characterized as a species in which large populations have been reduced suddenly to small size, it is reasonable to apply this standard to this species. That is, it is unlikely that previous selection has already purged recessive alleles from RCW populations. Instead, this species probably is quite vulnerable to this threat.

Effective size refers to an idealized population in which individuals mate randomly and all contribute equally to reproduction. In this hypothetical ideal population, all individuals pass on an equal number of their genes to subsequent generations. Effective size is a theoretical standard used to estimate the retention and loss of genetic variation in a real population. The effective population size itself is never measured directly; it is calculated using formulas based on genetic theory and demographic data collected from real populations.

The actual population size is almost always higher than the effective size, because several characteristics of animals and populations act to make the genetic contribution of individuals to subsequent generations unequal. For example, some pairs or individuals may consistently produce more offspring than others, and some individuals live longer than others. It is mainly this variation in reproductive success that makes effective size less than actual size.

Thus, it is possible to calculate the effective size of a population if its demography is known. Such calculations indicate that for RCWs, the actual population size needed to achieve an effective size of 50 individuals is 31 to 39 potential breeding groups, depending on the details of the demography of particular populations (Reed et al. 1988b, 1993). According to Franklin's (1980) suggestion that an effective size of 50 is necessary to withstand threats from inbreeding depression, stable or increasing populations of 40 or more potential breeding groups are not threatened by inbreeding depression.

In the absence of immigration, Daniels et al. (2000) found that a stable population of 50 to 100 or more breeding groups was necessary to avoid inbreeding depression. Thus, the work by Daniels et al. (2000) as well as Franklin's (1980) initial suggestion, suggest that stable or increasing populations of at least 40, and possibly as many as 100 potential breeding groups— with an immigration rate of 2 or more migrants per year—are potentially required to protect against inbreeding depression. In response to fragmentation and small population size, many small RCW populations since 1995 have been recipients of RCWs translocated from large populations to rapidly increase recipient population size and to reduce the risk of local extirpation, loss of genetic variation, and inbreeding depression (Costa and DeLotelle 2006, McDearman unpublished). For example, high hatching failure rates in the small Avon Park Air Force range population have been reduced following periodic translocations since 1998 (Schrott et al. 2010, Aldredge et al. 2016).

The population size necessary to avoid loss of genetic variation due to genetic drift, however, is much larger. Franklin (1980) first proposed that an effective size of 500 individuals would allow maintenance of long-term viability, because loss of genetic variation from drift would be offset by the creation of new variation through natural mutation. However, Lande (1995) argued that only populations with an effective size of over 5000 individuals can be expected to maintain viability in the absence of immigration, because not all mutations are beneficial. If the balance between loss of variability to drift and generation of variability by mutation is computed using only beneficial mutations, the much large figure of 5000 results. Others argue that an effective population size of 500 to 1000 individuals is sufficient (Franklin and Frankham 1998). At issue is the potential effects of harmful mutations: Franklin and Frankham (1998) consider these effects negligible, but others have suggested that slightly deleterious mutations are capable of causing population extinction even at effective sizes of several hundred (Lande 1994, Lynch et al. 1995, Lynch and Lande 1998). The debate will likely continue, but a reasonable conclusion is that only populations with actual sizes in the thousands, rather than hundreds, can maintain long-term viability and evolutionary potential in the absence of immigration.

Thus, without immigration, populations of RCWs that have reached recovery or management goals may still be susceptible to loss of genetic variability through genetic drift. One practical way to reduce this threat is to promote immigration, both natural (from support and other core populations) and artificial (from translocation). Sufficient connectivity among populations, in the order of 1 to 10 migrants per generation in each direction (0.25 to 2.5 migrants per year), can maintain genetic variation and long-term viability for the species (Mills and Allendorf 1996). As populations increase, natural dispersal among them will likely increase, but determining actual rates of natural immigration is a critical research need. A second practical way to reduce the effects of genetic drift is to increase population size and recover the species as quickly as possible. Loss of genetic variation increases with decreasing population size, but such loss also increases dramatically if populations remain small over time (Hartl 1988).

The most extensive population genetic data are from studies based on allozymes and random amplified polymorphic DNA (Stangel and Dixon 1995, Haig et al. 1994a, 1996), although updated investigations with microsatellite and mitochondrial DNA are in progress by U. S. Geological Survey. These data indicate most genetic variation occurs among individuals within populations, and genetic differences increase with geographic distance between populations with significant, though somewhat low, genetic structure among populations ($F_{ST} = 0.14 – 0.21$).

More recent genetic data compare mitochondrial DNA (mtDNA) sequences acquired from samples during 1992-1995 and 2010-2014 to a historical pre-1970 sample set, and microsatellite DNA for the 1992-1995 and 2010-2014 periods (Miller et al. in press) for RCWs in 3 regional groups (western, eastern, and Florida) and by ecoregions. The western group corresponds to samples from Texas, Oklahoma, Louisiana, Arkansas, and southwestern Mississippi. The eastern group represents Virginia, North Carolina, South Carolina, and Georgia near the South Carolina boundary. The Florida data set primarily are sites in the peninsula. The 8 ecoregions are East Gulf Coastal Plain, Mid-Atlantic Coastal Plain, South Atlantic Coastal Plain, Sandhills, South-Central Florida, Upper East Gulf Coastal Plain, Upper West Gulf Coastal Plain, and West Gulf Coastal Plain. Miller et al. (in press) report that genetic diversity as measured by number of mitochondrial haplotypes has been reduced between the pre-1970s and the 1992-1995 data sets with the loss of about 25-30% of haplotypes. However, no phylogenetically distinct mtDNA lineages appear to have been lost, and no additional losses were detected between the 1992-1995 and 2010-2014 periods. The pre-1970s mtDNA data indicate a largely panmictic rangewide population, from which significant genetic structure ($F_{ST} > 0$) develops among regions and ecoregions concurrent with a loss of diversity in the 1990s and afterwards, probably as a result of fragmentation and reduced gene flow. With microsatellites, significant genetic spatial structure also is apparent among the 3 regions and 8 ecoregions for the 1992-1995 and 2010-2014 periods. Current genetic structure (2010-2014), although significant, is generally low with F_{ST} estimates from 0.018 to 0.208 depending on the regional group, ecoregion, and sampling unit. The absence of detectable changes in genetic diversity or structure between the 1992-1995 and 2010-2014 periods indicate that RCW conservation management actions to increase population size and translocate RCWs to augment critically small populations that were included in these samples may have been important to reduce a further loss of genetic variation and development of more significant patterns of genetic differentiation and structure.

CHAPTER 3: SPECIES NEEDS FOR VIABILITY

In this chapter we consider the RCW's historical distribution, current distribution, and what the species needs for viability. We first review the historical and current information on the range, distribution and management of the species. We next review the conceptual needs of the species, including population resiliency, redundancy, and representation to support viability and reduce the likelihood of extinction.

Historical Distribution and Management

RCWs were once considered a common bird distributed across the southeastern United States. Reports published in the 1800s indicated they occurred at least in small numbers as far north as New Jersey. Given the historical distribution of its habitat and comments by early naturalists about its abundance, it is highly likely that RCWs originally were distributed fairly continuously over broad areas. The birds inhabited open pine forests of the southeast from New Jersey, Maryland and Virginia to Florida, west to Texas and north to portions of Oklahoma, Missouri, Tennessee and Kentucky (Jackson 1971).

RCWs are well adapted to the southern pine ecosystems that prevailed throughout the southeastern United States. Southern pine savannas and open woodlands once dominated the southeastern United States and may have totaled over 200 million acres at the time of European colonization (Conner et al. 2001a). Longleaf pine communities characterized the Atlantic and Gulf coastal regions, and covered an estimated 60 to 92 million acres (Wahlenburg 1946, Frost 1993, Ware et al. 1993, Landers et al. 1995). About one quarter of the longleaf communities also supported other pines such as loblolly, shortleaf, slash, and pond pine in various proportions depending on soil conditions, especially in transitional zones between the coastal plains and other physiographic regions (Frost 1993, Landers et al. 1995).

By the 21st century, longleaf forests had declined to less than 3 million acres (Landers et al. 1995), of which about 3% remains in relatively natural condition (Frost 1993). Little old growth remains, and virtually no longleaf forest has escaped changes in the natural fire regime (Simberloff 1993, Walker 1999). Shortleaf pine was prevalent outside the range of longleaf, especially on dry slopes and ridges in the Interior Highlands and Oklahoma, and has declined considerably (Landers 1991, Smith and Martin 1995). In the precolonial forests, loblolly pine was present as a minor component of riparian hardwood ecosystems or in association with shortleaf pine in some upland interior forests (White 1984, Landers 1991, Christensen 2000).

At the time of European colonization, the RCW had been estimated to have ranged from 920,000 (Costa 2001) to more than 1.5 million groups (Conner et al 2001a). By the last quarter of the twentieth century, Jackson (1978c) estimated the rangewide population at less than 4,000 groups and approximately 10,000 individuals. The RCW was designated an endangered species by the U. S. Bureau of Sport Fisheries and Wildlife in 1970 (35 Federal Register 16047). In the early 1990s, estimates placed the total population at 4,029 (James 1995) to 4,694 (Costa and Walker 1995) active clusters.

The species' precipitous decline was caused by an almost complete loss of habitat. Fire maintained old growth pine savannas and woodlands that once dominated the southeast, and on which the woodpeckers depend, no longer existed except in a few small patches. Longleaf pine ecosystems, of primary importance to RCWs, are now among the most endangered systems on earth (Simberloff 1993, Ware et al. 1993). Shortleaf (*P. echinata*), loblolly (*P. taeda*), and slash pine (*P. elliottii*) ecosystems, important to RCW outside the range of longleaf, also have suffered severe declines (Smith and Martin 1995).

Loss of the original pine ecosystems was primarily due to intense logging for lumber and conversion to agriculture. Logging was especially intense at the turn of the twentieth century (Frost 1993, Martin and Boyce 1993, Conner et al. 2001a). Two additional factors resulting in the loss of original pine systems in the 1800's and earlier were exploitation for pine resins and grazing by free-ranging hogs (*Sus scrofa*; Wahlenburg 1946, Frost 1993). Later, in the 1900s, fire suppression and detrimental silvicultural practices had major impacts on primary ecosystem remnants, second-growth forests, and consequently on the status of the RCW (Frost 1993, Ware et al. 1993, Ligon et al. 1986, Landers et al. 1995, Conner et al. 2001a). Longleaf pine suffered a widespread failure to reproduce following initial cutting, at first because of hogs and later because of fire suppression (Wahlenburg 1946, Ware et al. 1993).

Southern pine forests in the latter part of the twentieth century became very different from precolonial communities not only in extent, but also in species composition, age, and structure (Ware et al. 1993, Noel et al. 1998). Original pine forests were old, open, and contained a structure of two layers: canopy and diverse herbaceous groundcover. These forests were dominated by longleaf pine in the Coastal Plain, longleaf and shortleaf pines in the Piedmont and interior highlands, and slash pine *(P. elliottii var. densa*) in south Florida. Forests dominated by loblolly pine were restricted to a portion of southern Arkansas and perhaps eastern Virginia and extreme northeastern North Carolina (White 1984, Christensen 2000). In contrast, much of today's forest is young, dense, and dominated by loblolly pine, with a substantial hardwood component and little or no herbaceous groundcover (Ware et al. 1993, Noel et al. 1998).

Current Distribution and Management

The current distribution and abundance of RCWs is largely due to intensive management, including prescribed fire, artificial cavities, translocations, and other activities. RCWs now occupy a patchy distribution from extreme southern Virginia south to Florida and west to Texas and Oklahoma. Currently, the Service estimates there are at least 7794 active RCW clusters rangewide across 11 states distributed as 124 demographic populations from as small as one active cluster to as large as 858 active clusters (see Current Conditions chapter). From other active cluster data insufficient to delineate their respective demographic populations, there are at least 8,000 active clusters rangewide.

Components of the integrated recovery strategy developed in the late 1990s (Conner et al 2001a, Rudolph et al. 2004) became the key elements expressed in the Service's 2003 Recovery Plan to guide management practices that would enable managers to conserve and grow RCW populations. These practices are applied at varying degrees on RCW populations on federal, State, and private lands identified in the 2003 Recovery Plan; generally, where midstory condition, cavity availability, demographics and habitat fragmentation are addressed in site specific recovery and management plans, these populations have fared well and have grown. There have been gains in manageable habitat adjacent to some recovery populations, particularly where Department of Defense installations have acquired buffer lands by encroachment partnerships with conservation partners. Woodpecker populations relying on properties with no affirmative requirements or incentives to conserve habitat have declined due to loss of foraging and nesting habitat, fragmentation and loss of suitable cavities.

Needs of the RCW

For the purpose of this report, we define viability as the ability of the species to sustain populations in the wild over time. Species with greater numbers (redundancy) of healthy populations (resiliency), encompassing a broad array of ecological and genetic diversity in a spatial arrangement that maintains adequate gene flow (representation), are more likely to be viable. Using the Species Status Assessment framework (Smith et al. 2018a), we describe the species' viability by characterizing the status of the species in terms of its resiliency, redundancy, and representation. Key to assessing resilience is the delineation of demographic delineations, which we describe below.

Delineating Demographic Populations

For the RCW to maintain viability, its populations or some portion thereof must be resilient. Because resilience is measured at a population level, it is important to define populations in a biologically meaningful manner. Definitions of a species' population have varied widely in response to concepts, available data, and purpose (Waples and Gaggiotti 2006). In an ecological context, these definitions have broadly included individuals that occupy a specific geographical area and interbreed. More precisely, a population has been defined as one in which individuals interact demographically (Waples and Gaggiotti 2006). The history of RCW population definitions reflect initially broad concepts in response to limited data, with subsequent application of more specific genetic and demographic criteria.

Historical classifications of populations

RCW populations were initially and commonly described as number of clusters within a geographic area. Jackson (1971) provided one of the first estimates of a rangewide number of active clusters also referred to as a rangewide population by others (USFWS 1985). Other early RCW status surveys concerned number of clusters for particular properties such as different National Forests, military installations, National Wildlife Refuges, and states where the term population, when used, was applied at a property level or political unit (e.g. Lennartz et al. 1983).

In the Service's (1985) first revision of the RCW Recovery Plan, a RCW population for the purposes of recovery was defined relative to a minimally viable genetically effective population (N_e) of 500 adults (as proposed by Franklin 1980; Frankel and Soule 1981). The size of a genetically effective population is an important factor affecting the maintenance and loss of genetic variation. The RCW census breeding population corresponding to a genetically effective population of 500 at that time was thought to be 250 RCW "clans" (e.g. breeding groups), with reservations due to theoretical uncertainties about these estimates and the lack of other more substantial guidelines (USFWS 1985). Subsequent research identified that more than 500 RCW breeding pairs in a closed population could be required for a genetically effective population of at least 500 due to different genetic models and demographic variation (Reed et al. 1988b, 1993, Walters 1991). Moreover, the universal application of a N_e =500 rule of thumb as a viable population for any species was limited because the effective population size to maintain adaptive genetic variation may require up to 5000 individuals to purge deleterious genetic mutations and in consideration of other theoretical and empirical genetic factors (Lande 1995, Lynch et al. 1995, National Research Council 1995, Lynch and Lande 1988).

Although the theory and practice of conservation biology to assess population viability today integrates stochastic population demography and genetics more effectively, this early RCW population size objective stimulated spatially explicit RCW population size capacity assessments and management. The RCW capacity for a property, mostly estimated on federal lands, was generally evaluated on the basis of providing 200 – 250 acres of suitable foraging habitat for a RCW group (U.S. Forest Service 1995, Beaty et al. 2004) in accord with the Service's RCW foraging habitat guidelines at that time (USFWS 1989). Capacity estimates provided a reference for the ability of a property to achieve a recovery or management population size objective.

In 1995, the U.S. Forest Service was the first to apply an explicit distance function between

RCW groups to define, identify, and manage populations and subpopulations (U.S. Forest Service 1995). They defined and described a population as:

> "May be used interchangeably with the term genetic population. A population is an aggregate of groups which are close enough together to provide adequate genetic interchange through dispersal of juvenile RCW to ensure long-term genetic viability. With RCW, all groups separated by more than 18 miles of currently suitable habitat or 5 miles or more of currently unsuitable foraging habitat should be considered separate populations. These distances should be measured along the route of suitable foraging habitat linkage."

For an isolated subpopulation:

> "An isolated subpopulation is an aggregate of groups close enough to each other to provide significant interchange between individual groups, ensuring at least short-term viability. The subpopulations are close enough to other subpopulations to provide adequate interchange through dispersal of juvenile and adult RCW to offset mortality or other losses within adjacent groups. If an aggregate of groups is separated from other groups by 5 miles or more of currently suitable foraging habitat or 3 miles or more of currently unsuitable foraging habitat, they would be considered a demographically isolated subpopulation."

A subpopulation was considered a demographic unit by virtue of the predicted ability of RCWs to successfully disperse within a subpopulation to replace breeding vacancies or losses to other group members due to mortality. The ability to spatially define a subpopulation of RCW groups within 5 miles across suitable foraging habitat, and within 3 miles if separated by unsuitable habitat, generally reflected earlier research on RCW group dynamics and dispersal (Walters et al. 1988, Walters 1991). In contrast, the population definition was a genetic unit with greater distances and, presumably, less frequent dispersal events. It is not clear why, for populations, a distance of at least 18 miles across suitable habitat or 5 miles with unsuitable habitat was prescribed as a genetic unit. These population criteria appear to have been developed by expert opinion during a 1990 RCW Scientific Summit on the RCW and workshop funded by the National Wildlife Federation and conducted by the Southeast Negotiation Network (e.g. Jackson 1994, U.S. Forest Service 1995).

RCW recovery management by other agencies at that time incorporated similar delineation functions, at least conceptually, to identify and prioritize management. For instance, the first U.S. Army RCW guidelines in 1996 (U.S. Army 1996) included objectives for Army installations to develop RCW goals for populations, defined as aggregations of sufficiently close groups for genetic interchange and maintenance of genetic diversity. According to these guidelines, RCW installation population goals also were to include any RCWs on other federal, state or private lands demographically functioning as part of a regional population with the installation. Specific distance functions were not prescribed for genetic or demographic populations, but were subjects of consideration for the development of particular installation plans. Other agencies adopted strategies similar to or identical to those of the U.S. Forest Service for RCW conservation management (e.g. USFWS 1998, Marine Corps Base Camp Lejeune 2000).

The 2003 RCW Recovery Plan was a significant revision in response to substantial new science and management. Recovery population size objectives and criteria were formulated as 39 separate primary core (13), secondary core (10), and essential support demographic populations (16), with other important and significant support populations distributed sufficiently within and across physiographic regions to promote genetic viability and reduce the risk adverse impacts from catastrophic hurricanes. As reviewed in the Plan, RCW populations functioned as demographically closed populations due to infrequent long distance dispersal. Territory densities or distances among territories were not defined to explicitly categorize demographic populations. However, the fact that dispersal occurs over short distances was inherent in the recommended strategy to manage populations by aggregating multiple RCW groups to the extent possible within 3.2 km (2 miles).

Recovery population size objectives, in contrast to the first 1985 revision of the recovery plan (USFWS 1985), were specific to particular properties and organizations. Each population was expected to function as a single demographic population when the future population objective was attained, but not because of a spatial analysis of the predicted location and distances between all future RCW territories. Instead, the future population size capacity was identified from an existing agency management plan or estimated with the best available habitat data according to estimated future number of RCW clusters in contiguous habitat, typically at 200 – 250 acres for each RCW group. These estimated future RCW densities were expected to function demographically based on RCW group dynamics known at that time and now. Each demographic population was identified by its constituent properties, when more than one, and the managing agencies or organizations. Of the 39 populations designated for recovery, the properties for 4 populations were recognized as sufficiently separated that, at recovery, they may not function as demographically single populations (Angelina-Sabine Primary Core, Coastal North Carolina Primary Core, Osceola-Okefenokee Primary Core, and Northeast North Carolina-Southeast Virginia Essential Support).

RCW status after the 2003 recovery plan, when reported and monitored as number of active clusters for designated recovery properties, has been associated with demographic population size. Similarly, the status of other “populations” as inventoried and reported at a property level has been at least implicitly recognized as demographic populations. At any particular time, however, the actual number and distribution of RCW territories on a particular property may not represent a single demographic population. For instance, the identification of small populations suitable as RCW translocation recipients in the Western Range Translocation Cooperative and Southern Range Translocation Cooperative since 1995 has been based on the spatial distribution of active clusters as demographic units. Small populations classified as suitable translocation recipient candidates with less than 30 potential breeding groups have been identified as those with aggregations of active clusters separated by no more than 4.8 km (3 miles). In other instances, demographic population size and structure has been assessed by site specific dispersal data, group dynamics, the distribution of active clusters, spatially explicit individual based population models, and other methods for a variety of management, conservation, and regulatory purposes, including Fort Benning (Walters et al. 2011, Bruggeman 2013) Fort Bragg (Walters et al. 2006, 2011) Eglin Air Force Base, Marine Corps Base Camp Lejeune (Walters and Priddy 2005, Walters et al. 2011), Savannah River Site (Walters et al. 2002c), and Plum Creek Timber properties (Walters and Priddy 2005).

Current population delineation

The approach and method used to delineate demographic populations for the SSA is based on the importance of demographic population size for resilience and builds upon the legacy of circumscribing a demographic population. Instead of relying on the census or estimated total number of active clusters for each property from various sources, we requested current or most recently available Geographic Information System (GIS) data for all active clusters from property biologists and managers to spatially delineate populations. We defined a RCW demographic population as the aggregation of RCW clusters/territories where a breeding vacancy at any territory is likely to be replaced by a RCW from a territory within the delineated population. Because of this definition, dispersal is a critical factor in delineating demographic populations, particularly dispersal to fill breeding vacancies.

RCW dispersal distances and social, environmental, and genetic factors affecting dispersal have been evaluated most extensively by data from long-term studies of a virtually completely banded population in the North Carolina Sandhills and Marine Corps Base Camp Lejeune (e.g. Walters et al. 1988a, Walters et al. 1992a, Daniels and Walters 2000b, Pasinelli and Walters 2002, Pasinelli et al. 2004, Kesler et al. 2010). Overall, median dispersal distances of juvenile males, helper males, juvenile females, and helper females, respectively, were 2.94 (1.83), 1.27 (0.79), 3.31 (2.06), and 1.88 (1.17) km (miles) (Kesler et al. 2010). Dispersal events were movements by territorial non-breeders to a new territory where a breeding position was acquired the following breeding season.

We use a juvenile female dispersal distance metric to delineate demographic populations. Helper males, when present, commonly acquire the breeding vacancy created by the death of the breeding male. Juvenile females do not replace the breeding female, their mother, on their natal territory to avoid incest. Juvenile females disperse except in rare instances when they remain as nonbreeding helper. Thus, the continuity of potential breeding pairs at territories is most sensitive to effective dispersal of juvenile females, although the smaller class of floater females may also fill breeding vacancies. Female juvenile RCWs disperse following extraterritorial forays from their natal territory to explore and interact with other groups, with maximum foray distances from 6-9 km (3.7 – 5.6 mi, Figure 16) (Kesler et al. 2010). Juvenile females also are more sensitive to crossing open nonforest gaps (water, fields, etc.) during dispersal. Gaps greater than 150 meters are not absolute barriers during forays, but the probability of crossing gaps greater than 150 meters (492 feet) diminishes substantially with increasing gap size with rare movement across gaps greater than 600 meters (1969 feet) (Kesler et al. 2010, Walters et al. 2011, Bruggeman and Jones 2014). Forays and dispersal of juvenile females from their natal territory through a complex habitat matrix also is affected by forest habitat conditions. In general, RCWs tend to prefer and more readily move thru habitat similar in structure and composition to that used for foraging, while avoiding areas with dense midstory cover (Moody et al. 2011, Trainor et al. 2013).

Because forays greater than 6 km are rare for female juvenile RCWs, we delineated RCW demographic populations using the GIS provided by property managers as the aggregation of RCW clusters/territories ≤6 km from other nearest neighbor active clusters/territories within the delineated population. Accordingly, each delineated population consists of a population size in terms of number of active territories. The 6 km distance is the 95% percentile of all observed juvenile female forays by Kesler et al. (2010). The 6 km function corresponds with the perceptual distance, derived from the same data, at which juvenile females will compete for or acquire a breeding vacancy in the RCW Decision Support System (DSS) spatially explicit individual-based population simulation model by Walters et al. (2011) and other derived RCW population models (e.g. Bruggeman and Jones 2014). We examined aerial imagery to identify nonforest gaps greater than 600 m (0.37 miles) along a straight line distance between neighboring active clusters within 6 km for our SSA demographic delineations. We delineated separate populations where significant gaps were identified and connectivity by movement around the gap, but within a 6 km movement distance, would require a highly circuitous route. We did not account for potential effects of a forest habitat matrix with a dense midstory or low canopy height that could reduce or impede movement (Trainor et al. 2013). The identification of these and related habitat features require substantial data from stand level forest inventories, LiDAR or other sources that are not available for the extensive habitat associated with the large number of delineated populations. Furthermore, transforming forest habitat data even if comprehensively available to an appropriate nonlinear movement resistance probability surface and model (e.g. Trainor et al. 2013) would be beyond the scope of this SSA.

Delineation of populations according to the 6 km distance function was vetted through the RCW SSA expert team consisting of scientists, biologists, and managers from various organizations with knowledge of RCW conservation biology, forest habitat management and restoration, fire ecology, and agency or organization programs. The application of a 6 km juvenile foray distance, in contrast to a shorter median distance, will in some instances delineate larger demographic populations. The use of a median distance, whether for forays or actual dispersal, would tend to underestimate the size of some demographically connected populations. The strength of demographic connectivity in 6 km delineated populations with sparse territory aggregations may be overestimated.

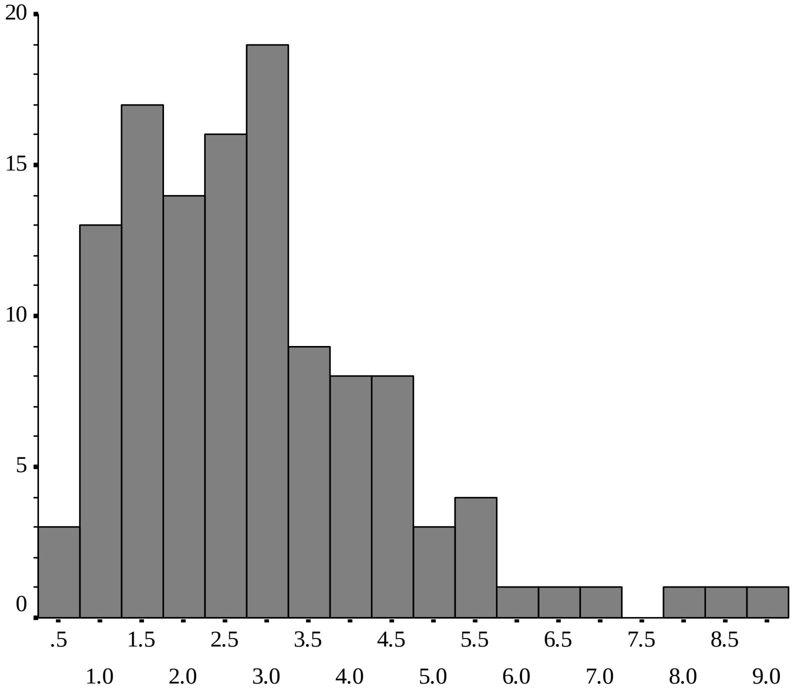


Figure 16. Foray distances of juvenile female RCWs observed by radiotelemetry on western Fort Bragg. From SERDP project RC-1471 (Kesler et al. 2010).

Population Resiliency

For the RCW to maintain viability, its populations or some portion thereof must be resilient. Resiliency to various factors such as routine annual temperature variation, inbreeding depression, etc. must be assumed for populations prior to human interference. In addition, stochastic factors that have the potential to affect RCW include a variety of habitat disturbances. Other factors that influence the resiliency of RCW populations include key management factors that influence habitat elements and population level factors. Influencing all of these factors are elements of RCW ecology (e.g. dispersal and reproductive success) that determine whether populations can grow to maximize habitat occupancy, thereby increasing resiliency of populations. Unfortunately, the lack of demographic data from populations that have not benefited from human management precludes distinguishing between natural and ‘artificial’ resiliency. These influences, factors and habitat elements are discussed below (Figure 17).

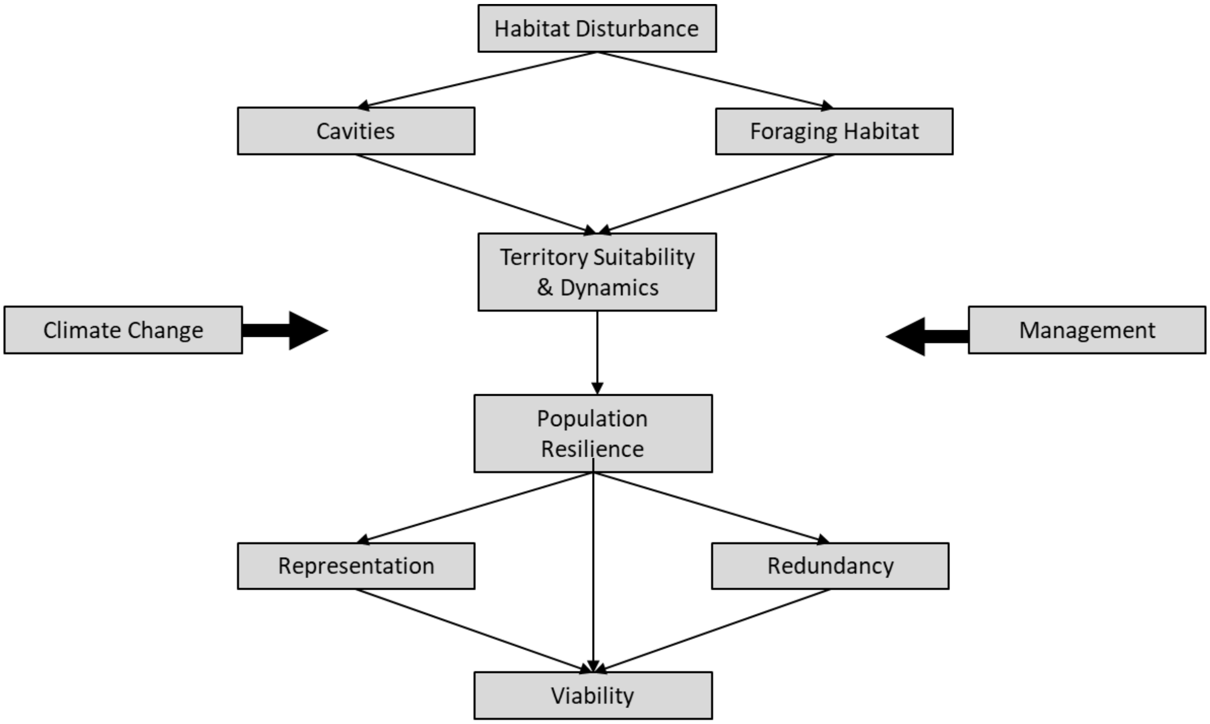


Figure 17. Main influence diagram showing factors and influences which underlie RCW resilience measures.

Habitat Disturbance

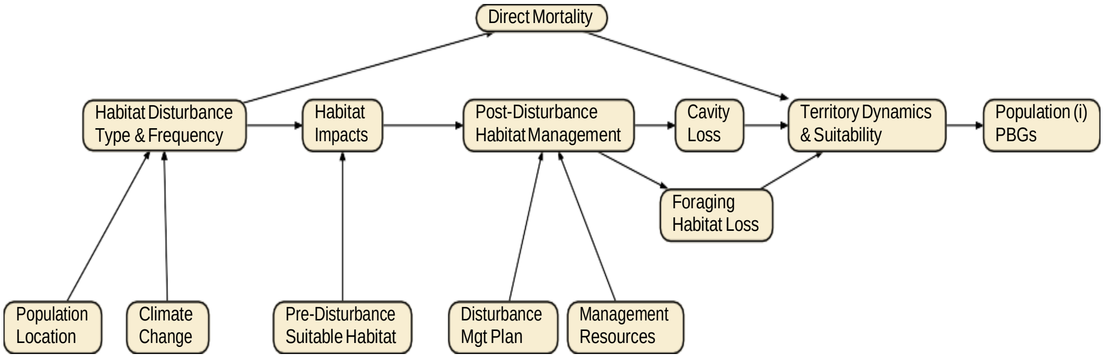


Figure 18. Influence diagram showing elements of habitat disturbance impacting RCW population resilience in terms of population size (PBGs).

Key to the persistence of RCW populations is the availability of cavities and foraging habitat. Impacting the availability of these key habitat features are a variety of disturbances. We briefly discuss a few of the key disturbances here, but have an expanded discussion in the section "Influences on Viability".

Hurricanes and Other Storm Events

Hurricanes, tropical depressions, tornados, severe thunderstorms, and ice storms are natural meteorological disturbances that very large, extensive and naturally resilient RCW populations during pre-settlement conditions presumably bounced back from over time. However, the vulnerability of populations to hurricanes and other storms is greater now due to a reduction in population size and fragmentation. Depending on severity, storms can significantly damage or destroy pines currently used for cavities and foraging habitat. Other than ice storms, these are wind events that can snap limbs, boles, and blow down stranding trees. Ice storms can cause the same effects, although by the accumulated weight of frozen precipitation. Storms directly can cause RCW mortality, as has been observed by dead individuals in natural and artificial cavities located where the trunk or bole broke, and within cavities from downed pines. These storms also may damage or destroy pines not currently used for cavities or foraging habitat, but are resources for future cavities and foraging habitat. The frequency and intensity of these disturbances to cavities and foraging habitat may be affected by pre-storm habitat conditions and the location of populations. For instance, coastal populations are more likely to experience more frequent and intense hurricanes than inland populations. Post-disturbance management can reduce adverse impacts to cavities and foraging habitat. For instance, artificial cavities may be installed. Down and damaged pines and other debris creating heavy or hazardous fire fuel loads can be salvaged, mulched, and treated to reduce fire hazards and support frequent prescribed fire to sustain remaining foraging habitat.

Southern Pine Beetles

The southern pine beetle, *Dendroctonus frontalis*, is a species of bark beetle native to the forests of southern United States, Mexico, and Central America, which disrupts the flow of nutrients into pine trees, killing the tree within months. Southern pine beetle outbreaks can be minor or locally significant by killing cavity trees and other pines used for foraging. The impact of southern pine beetles on RCW is on the cavity trees, not the birds—at least not directly. As with hurricanes, forest stand composition is a major pre-disturbance factor affecting the severity of the impact of these beetles. For example, loblolly and short leaf pines are more susceptible to infestation, as they produce less resin compared to longleaf pine, and resin secretion provides defense for these trees to initial attacks by the pine beetle. As with all habitat disturbance types, the presence of sufficient management resources and a management plan is critical to a sufficient response to minimize the impacts of an outbreak. Depending on the extent and severity of the outbreak, stands must be thinned to stop the spread, and this thinning can cause direct loss of active clusters, but the long term benefits of stopping the outbreak often outweighs the short term impacts of losing a few clusters.

Other Disturbance Types

There are many other disturbance types that have the potential to impact RCW habitat, and therefor population resilience. These types include, but are not limited to wildfire, wildlife urban interfaces, invasive species, drought, sea level rise, and kleptoparastism. We discuss these in depth in the section on "Influences on Viability", but the themes remain the same. These disturbances can have direct and/or indirect impacts on the availability and quality of cavities and foraging habitat. The condition of that habitat pre-disturbance and the availability of resources and a management plan greatly affect the ability of populations to "bounce back" from these disturbances. This highlights the management reliance of this species.

Cavities

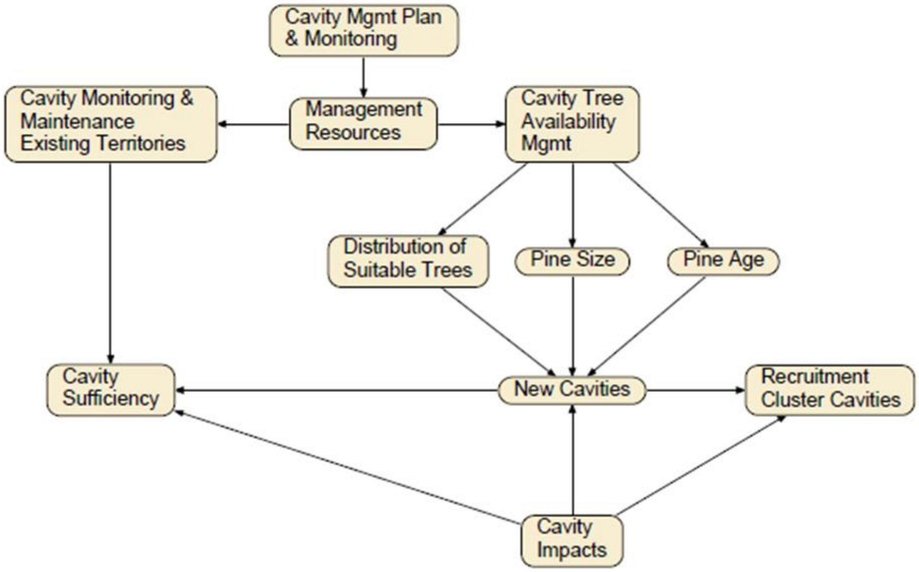


Figure 19. **C**avity influence diagram.

Loss of cavities and cavity trees was a primary cause of the decline of RCW, and is currently a substantial threat. RCW will abandon clusters if sufficient suitable cavities are not available. Cluster abandonment can lead directly to population extirpation (Costa and Escano 1989), because populations of RCW are regulated by the number of potential breeding groups rather than by annual variation in reproduction and survival (Walters 1991), and because natural formation of new clusters is very slow at least under conditions of relatively young forests and small populations. Therefore, cavity management is absolutely critical to the conservation of most populations. As a result, these are the primary conditions for which we have data on cluster and population persistence.

As discussed in the Species Biology section, cavity availability is a function of the distribution of suitable trees, pine size, pine age, and other factors. Although RCW excavate their own cavities under certain conditions with suitably available old pines, the advent and use of artificial cavities (Copeyon 1990, Copeyon et al. 1991, Allen 1991, Taylor and Hooper 1991) have revolutionized management of RCW. Prior to their development, biologists were unable to address the severe limitation in cavities due the loss of old pines impacting most populations, and therefore had little ability to slow, much less reverse, the decline of the species. With the advent of artificial cavity technology, cavities and entire clusters can be provided. In combination with aggressive habitat management, artificial cavity management can stabilize and increase populations.

Artificial cavities have not always been used effectively, thus a good cavity management plan with associated monitoring is critical to the success of a cavity management program. Widespread and haphazard installation of artificial cavities can have negative impacts on RCW and their potential cavity trees, and misdirects valuable management efforts and funds. Before artificial cavities are installed, managers should have a clear understanding of population dynamics in this species, especially the role of cavities and the effects of spatial structure on population growth or decline. In addition, managers need to be well versed in the benefits and drawbacks of the various installation methods, so that they know what to expect of cavities already installed in their populations and can choose the appropriate method for additional cavities. Finally, proper maintenance of artificial cavities to prevent decay, clean debris, and replace artificial cavities is essential (e.g., Montague et al. 1995, Saenz et al. 2001).

Carrie et al. (1998) found that group size of RCWs in Louisiana increased with the number of cavities provisioned, and recommended a minimum of 3 to 4 suitable cavities per cluster. Results of the study more clearly supported the use of 4 suitable cavities rather than 3 as a minimum. A minimum of 4 suitable cavities per cluster has also been the traditional policy of the Service. A suitable cavity has a single entrance, an entrance tunnel that is not enlarged, a cavity chamber that is not enlarged, a solid base, and is dry and free of debris. In addition, the cavity plate must not contain large amounts of dead wood (Carrie et al. 1998). Relict, enlarged, or any suspect cavities are not considered suitable for use by RCWs.

Ultimately, the goal of proper cavity management is to provide sufficient quality nesting habitat for the RCW, thus increasing the resiliency of populations. Cavity management is critical for managing exiting groups, but in order to grow populations and ultimately recover the species, new groups of woodpeckers must be induced within existing populations. This is done through use of recruitment clusters with sufficient cavities in association with compatible forest management to establish suitable foraging habitat and a source of pines of sufficient size and age for artificial cavities. Restoring and maintaining suitable foraging habitat without recruitment clusters is inadequate to induce new group formation at rates required for recovery. We discuss recruitment clusters in the section on territory suitability and dynamics.

Foraging Habitat

Much of the background on foraging habitat for RCWs can be found in the Species Biology

Section of this report. Ultimately, RCWs must have sufficient nesting (i.e. cavity management) and foraging habitat to persist. Foraging habitat can vary greatly, particularly by physiographic region, but in general managing for good foraging habitat is managing for the development of old pines with mid-story control, typically through the application of prescribed fire.

Supplying good quality foraging habitat is a critical aspect of RCW recovery, especially over the long term, as immediate threats from cavity and cluster limitation are reduced. Our understanding of what constitutes good quality foraging habitat comes from a synthesis of research into selection of foraging habitat and effects of habitat characteristics on group fitness. RCWs require foraging habitat that is suitable in both quantity and quality.

Both habitat selection and group fitness are influenced by the structure of the foraging habitat. Important structural characteristics include (1) healthy groundcovers of bunchgrasses and forbs, (2) minimal hardwood midstory, (3) minimal pine midstory, (4) minimal or absent hardwood overstory, (5) a low to intermediate density of small and medium sized pines, and (6) a substantial presence of mature and old pines. Natural hardwood inclusions also occur or would be expected by foraging habitat management (USFWS 2003). Thus, the quality of foraging habitat is defined by habitat composition and structure. Although geographic variation in habitat types exist, these structural characteristics of good quality habitat remain true for all geographic regions and habitat types with frequent fire. An unusual exception are the unique pond pine, loblolly pine and hardwood habitat types on wet organic soils in northeast North Carolina and southeast Virginia (Carter and Brust 2004, Smith et al. 2018b).

Quantifying habitat structure (and thus habitat quality) is more complex than simply requiring a given amount of habitat or number of trees, because habitat structure is measured by multiple variables. Current Service (2003) guidelines for managing foraging habitat are based on the quantification of structural characteristics to the best of current abilities. Frequent fire can facilitate the restoration and maintenance of all but one of these structural characteristics (mature and old pines), and may provide further benefits by increasing the availability of nutrients. In addition, appropriate silvicultural methods will protect, throughout the landscape, the mature and old trees on which RCWs thrive.

Territory Suitability and Dynamics

Much of the background on territory suitability and dynamics for RCW can be found in the Species Biology Section of this report. Here we discuss those general factors related to territory suitability and dynamics that are critical to resilience of RCW populations: recruitment clusters, population size, and the spatial arrangement of active clusters.

Proper management of the nesting and foraging habitat of existing populations is a prerequisite for population increase, but recent research and experience strongly indicate that management of existing groups and foraging habitat by itself has not been sufficient to bring about the rates of increase necessary for recovery. Because population dynamics of RCWs are regulated by the number of potential breeding groups, substantial increases in population size are best obtained through continued addition of recruitment clusters. Therefore, guidelines for the use of recruitment clusters in all populations being managed for increasing population size have been developed (USFWS 2003). Recruitment clusters are clusters of artificial cavities in habitat containing mature and old pines, with little or no hardwood midstory and a healthy grass and forb groundcover. Key to the success of recruitment clusters are factors such as number of recruitment clusters, placement of recruitment clusters near active clusters, and proper provisioning of sufficient nesting, roosting, and foraging habitat. Finally, as with any management action, population monitoring is critical. Only through accurate monitoring can we determine the success and failure of our management actions, and adapt these actions accordingly. Appropriate intensity of monitoring varies with population size, role in recovery, and management objectives.

As would be expected, in general, as population size of RCWs increases, so does the resilience of that population. Although factors such as territory aggregation and clustering, habitat quality, and other factors complicate assessing resilience with population size alone, there are some general guidelines for assessing population resilience based on number of active clusters and results from validated spatially explicit individual-based RCW population models (SEPMs) (USFWS 2003). The SEPM and simulations by Walters et al. (2002b) and subsequent applications (Daniels et al. 2000, Schiegg et al. 2006) identified effects of population size, density, inbreeding depression and stochastic demographic and environmental effects on persistence in suitable habitat without cavity or other habitat limitations and without active management for future population growth by recruitment clusters. Population size and growth were measured as number of active clusters (e.g. occupied territories). Simulated population growth was possible only by pioneering and budding in habitat with suitable old and well distributed pines for natural cavity excavation. Demographic, dispersal, and RCW group parameters were derived from long-term intensively monitored populations in the Sandhills and Lower Coastal Plain of North Carolina.

RCW populations of 30 or fewer active clusters are critically small and the most vulnerable to extirpation. If they are not intensely managed, there is a good chance the population would be extirpated in a relatively short time. Adverse demographic effects of inbreeding depression under natural conditions and fragmentation further increase vulnerability to extirpation.

Groups between 30-100 active clusters also need to be managed well without limitations to cavities and foraging habitat, but if clustered in a relatively well aggregated form, they can persist for longer periods of time. However, these populations remain highly vulnerable to declining growth, inbreeding depression and extirpation, particularly in smaller or larger sparse populations. The most aggregated largest populations should be relatively more persistent with long-term average growth rates near 1.0, but with a slow overall decline.

Populations of 100-250 active clusters represent a transitional resilience class from smaller to larger populations. Potential breeding pairs may become genealogically related and closely related as inbreeding accumulates in the smaller populations without adequate immigration leading to inbreeding depression, declining populations, and a greater risk of extirpation. The smaller and intermediate populations with a sparse density without inbreeding depression likely will experience a slow decline, but without future absolute extirpation in 25 to 50 years because some territories should survive due to population size and the rate of decline. Large sparse, moderately dense and dense populations at or near 250 potential breeding groups in this category should be relatively stable or nearly so.

Most populations of 250-500 or more active clusters are expected, on average, to be stable except for the smallest and sparsely aggregated that can have growth rates slightly less than 1.0 and a slow decline. Adverse demographic effects of inbreeding depression are not expected. Periodic impacts of category 1 and 2 hurricanes to populations in the Lower Coastal Plain and peninsular Florida would reduce population size, but not cause extirpation over short intervals. Larger hurricanes, particularly category 4 or 5 storms, with a direct strike may significantly reduce population size and potentially cause extirpation in smaller populations. The largest populations of more than 500 are the most resilient, although very few populations of this size or future potential are expected because of the limited availability of large, contiguous landscapes owned by agencies or other entities engaged in RCW recovery for such populations. For example, a population of 500 active clusters with territories of 100 to 200 acres each would minimally require 50,000 – 100,000 acres of suitable habitat. The actual landscape to support such populations is greater because of the distribution and acreage of other naturally intervening unsuitable habitat types. A caveat on these larger populations: with little to no management, particularly prescribed fire and artificial cavity management, habitat can degrade quickly and the population will lose resilience rapidly. RCW populations are still dependent on artificial cavities.

Resilience: Potential Breeding Groups and Associated Growth Rates

Resilience is a population level attribute, and for the purposes of this SSA, represents a population’s ability to withstand deterministic and stochastic events of limited intensity and frequency arising from a variety of factors. As described previously, there are several population, habitat, and management factors underlying current RCW resilience, as well as many potential influences impacting those factors (e.g. hurricanes, pine beetles, etc.). Ultimately, RCW population resilience can be measured as the number of potential breeding groups in a population and that population's growth rates. A potential breeding group is an adult female and adult male that occupy the same cluster, with or without 1 or more helpers, whether or not they attempt to nest or successfully fledge young. As previously discussed, in general, the greater the number of potential breeding groups in a population, the greater the resilience of that population. Also important in assessing the resilience of a population is the associated growth rate. Positive or negative growth rate reflect underlying demographic parameters known to be important to RCW, such as fledging rate and nest success, as well as the availability of suitable habitat and management. The Recovery Plan (USFWS 2003) recommends that RCW populations managed for recovery increase at an average rate of 5 percent per year toward the population and management objective. Measures of population growth (r, λ) over time also dampen random annual fluctuations. Ultimately, a resilient population of RCW has a large number of potential breeding groups and a positive growth trajectory where suitable unoccupied habitat is available and managed for growth.

Species Representation

Representation provides the ability of the species to adapt to physical (e.g., climate conditions, habitat conditions or structure across large areas) and biological (e.g., novel diseases, pathogens, predators) changes in its environment presently and into the future; it is a proxy measure for the evolutionary capacity or flexibility of the species. Representation is the range of variation found in a species, and this adaptive diversity is the source of species' adaptive capabilities. RCW adaptive diversity can be thought of as the amount and spatial distribution of genetic and phenotypic diversity. By maintaining these 2 sources of adaptive diversity across a species' range, the responsiveness and adaptability of a species over time is preserved.

Genetic diversity is the foundation for adapting to changing environmental conditions (Hendry et al. 2011). For adaptation to occur, there must be variation upon which to act (Lankau et al. 2011). An ongoing study by U. S. Geological Survey will provide new information in the near future, parts of which (Miller et al. in press) have become available.

The most extensive population genetic data are from studies based on allozymes and random amplified polymorphic DNA (Stangel and Dixon 1995, Haig et al. 1994a, 1996), although updated investigations with microsatellite and mitochondrial DNA are in progress by U. S. Geological Survey. Recent study by mitochondrial DNA (mtDNA) samples from pre-1970, 1992-1995, and 2010-2014 and microsatellite data from regions and ecoregions also are available (Miller et al. in press), as reviewed in Chapter 2. As reported by Miller et al. (in press) genetic diversity has been reduced, although no phylogenetically distinct lineages appear to have been lost. The pre-1970s mtDNA data indicate a largely panmictic rangewide population, from which significant genetic structure ($F_{ST} > 0$) develops among regions and ecoregions concurrent with a loss of diversity in the 1990s and afterwards, probably as a result of fragmentation and reduced gene flow. The magnitude of contemporary genetic structure identified by Miller et al. (in press), relative to pre-1970 conditions, is similar to that by Stangel and Dixon (1995) and Haig et al. (1994a, 1996) in the mid-1990's. With microsatellites, significant genetic spatial structure also is apparent among the 3 regions and 8 ecoregions for the 1992-1995 and 2010-2014 periods. Current genetic structure (2010-2014), although significant, is generally low with F_{ST} estimates from 0.018 to 0.208 depending on the regional group, ecoregion, and sampling unit. The absence of detectable changes in genetic diversity or structure between the 1992-1995 and 2010-2014 periods indicate that RCW conservation management actions to increase population size and translocate RCWs to augment critically small populations that were included in these samples may have been important to reduce a further loss of genetic variation and development of more significant patterns of genetic differentiation and structure. Thus, RCW representation in populations across regions and ecoregions remains important to support genetically effective dispersal to avoid further losses of diversity and increasing patterns of genetic differentiation contrary to that most likely for this historically abundant and wide-ranging species.

We also evaluate representation through variation in habitat types or patterns of phenotypic diversity. Phenotypic diversity (the physiological, ecological, and behavioral variation expressed by RCW) is important for adapting to changes in environmental conditions. Phenotypic variation determines how organisms interact with their environment and how they respond to selection pressures (Hendry et al. 2011). The degree of phenotypic variation is determined by the diversity of physical and biological pressures to which organisms are exposed, which vary across spatial and temporal scales. As such, species that span multiple environmental gradients are expected to harbor the most phenotypic and genetic variation (Lankau et al. 2011, p. 320). Thus, preserving the breadth of phenotypic diversity of RCWs requires maintaining populations across historical ecological, climatic, latitudinal and longitudinal gradients to increase the likelihood that the species will retain the potential for adaptation over time. RCW representation is, therefore, described as having resilient and redundant populations widely distributed across a breadth of ecological conditions.

For the RCW, we characterize representative units by using ecoregions, and measure representation as the presence of resilient populations within each of the delineated representative units. RCWs inhabit a number of ecoregions/physiographic provinces across their range. Ecoregions (physiographic provinces; e.g. Bailey 1983, Bailey et al. 1994) are a system of classification based on physiography, the study of the natural features of the earth's surface. Important to physiography and the designation of ecoregions are characteristics of land formation, climate, air and sea currents, and distribution of flora and fauna. Ecoregions are a more finely grained system of classification than the world biome system (Clements and Shelford 1939), for example, but not as fine as classifications according to ecosystems or communities.

Ecoregions can be used to represent varying habitat, climatic, and edaphic factors that have likely influenced species evolution over time. Although the natural boundaries of ecoregions are generally gradual rather than distinct, distinct boundaries have been delineated for purposes of RCW recovery (USFWS 2003), as they reflect broad areas within which local adaptations and genetic coadaptation have likely occurred. Genetic coadaptation is the evolution of gene complexes that together impart greater fitness than the sum of each individual gene's contribution. A coadapted gene's effect depends on the presence of 1 or more other genes (Templeton et al. 1986). Thus, major objectives in the use of ecoregions are to identify likely genetic variation and to assure that this variation is conserved to the fullest extent possible.

Ecoregions can act as an appropriate proxy for several factors likely to influence the adaptive capacity of RCWs across the landscape. First, ecoregions are known to be composed of differing dominant or prevailing pine types. From the shortleaf pine dominated systems of the Ouachita Mountains, the pond pine pocosin dominated regions of northeast North Carolina and southeast Virginia, the south Florida slash pine dominated areas in the southern Florida Peninsula, and the many other regions dominated by longleaf and loblolly pine, differences in historical and contemporary dominant plant communities have the potential to confer representation, or diversity, in RCWs, and thus the capability of adapting to changes in its environment. Ecoregions with RCWs also occur along a long latitudinal and longitudinal gradient. Geographic patterns of life history variation are evident with greater RCW adult survival and lower productivity in coastal populations, and lower adult survival and greater productivity inland. RCW group size generally decreases in the southern and western range (McKellar et al. 2014). Also, climate change has the potential to influence productivity and the distribution of vegetative communities, such as longleaf pine systems, through anticipated changes in temperature and precipitation patterns. RCW females that lay eggs earlier in warmer climates and in response to increasing temperature from climate change are more productive, but inbred and inexperienced females lay later and are less productive (Schiegg et al. 2002). This underlies the importance of having RCW populations represented throughout the latitudinal and longitudinal extent of the species range.

Below we generally describe 12 ecoregions RCWs currently inhabit (Figure 20): Cumberland Ridge and Valley, East Gulf Coastal Plain, Florida Peninsula, Gulf Coastal Prairies and Marshes, Mid-Atlantic Coastal Plain, Ouachita Mountains, Piedmont, Sandhills, South Atlantic Coastal Plain, Upper East Gulf Coastal Plain, Upper West Gulf Coastal Plain, and West Gulf Coastal Plain. We include the Tropical Florida region (Figure 20) in the Florida Peninsula to provide consistent reference to the Peninsula as applied in the 2003 RCW recovery plan (e.g. South/Central Florida), while noting this is the most extreme southern region.

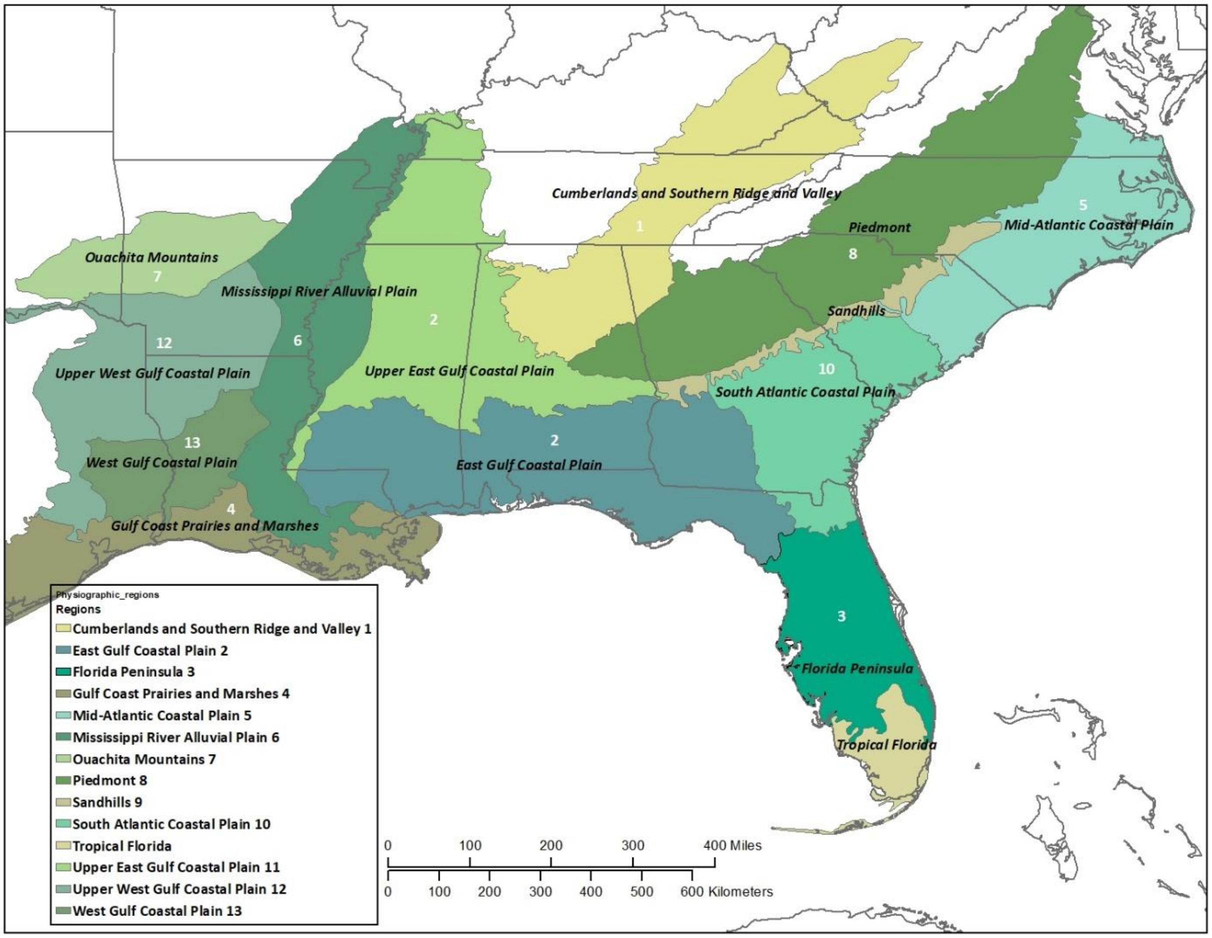


Figure 20. RCW ecoregions.

Our use of ecoregions as defined in the 2003 recovery plan provides a comparative reference for past, current and estimated future RCW conditions for representation. These regions are intermediate in resolution between physiographic or ecoregion classifications that are more coarse and those with much finer geographic resolution. Differences in various ecoregion classifications reflect the roles of geology, topography, landform, soils, vegetation, climate, biota and other features relative to the intended purposes of the product (Omernik and Griffith 2014). For example, the broad provinces by Bailey (2016) for the Outer Coastal Plain and Southeastern Mixed Forest Province (Figure 21) extend over a very large area without differentiation of geographic, climatic and vegetation units considered important features of RCW representation. The U.S. Forest Service's ECOMAP provinces are similar to the Bailey provinces, but with a finer scale classification of numerous ecological sections within provinces (Figure 22, Cleland et al. 1997, 2007). RCW ecoregions (Figure 20) for the West Gulf Coastal Plain, Upper West Gulf Coastal Plain, Ouachita Mountains, and East Gulf Coastal Plain correspond closely with respective ECOMAP sections (Figure 22). The RCW Piedmont ecoregion is fundamentally the same as the Environmental Protection Agency's Piedmont ecoregion in the EPA Level III ecoregion classification (Figure 23, Omernik 1987, Omernick and Griffith 2014). The RCW

Mid-Atlantic Coastal Plain ecoregion is similar, though broader than, the EPA Level III Middle Atlantic Coastal Plain ecoregion. The RCW Florida Peninsula ecoregion is the same as the EPA Level III Southern Coastal Plain ecoregion, but only as restricted to the peninsula. The RCW South Atlantic Coastal Plain unit includes elements of EPA Level III ecoregions and ECOMAP sections.

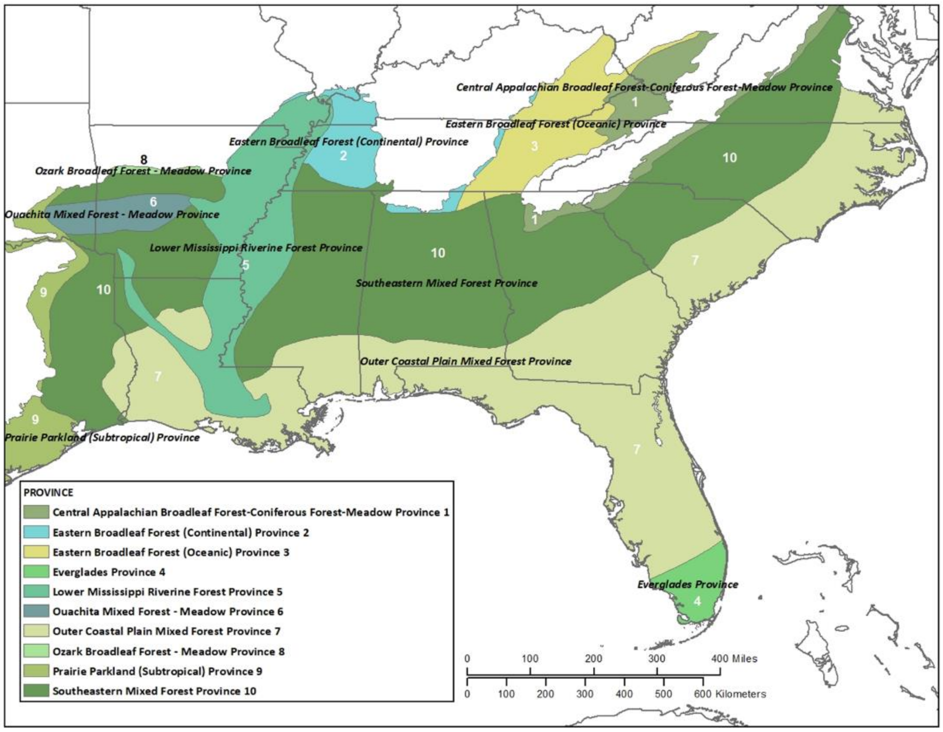


Figure 21. Bailey physiographic provinces.

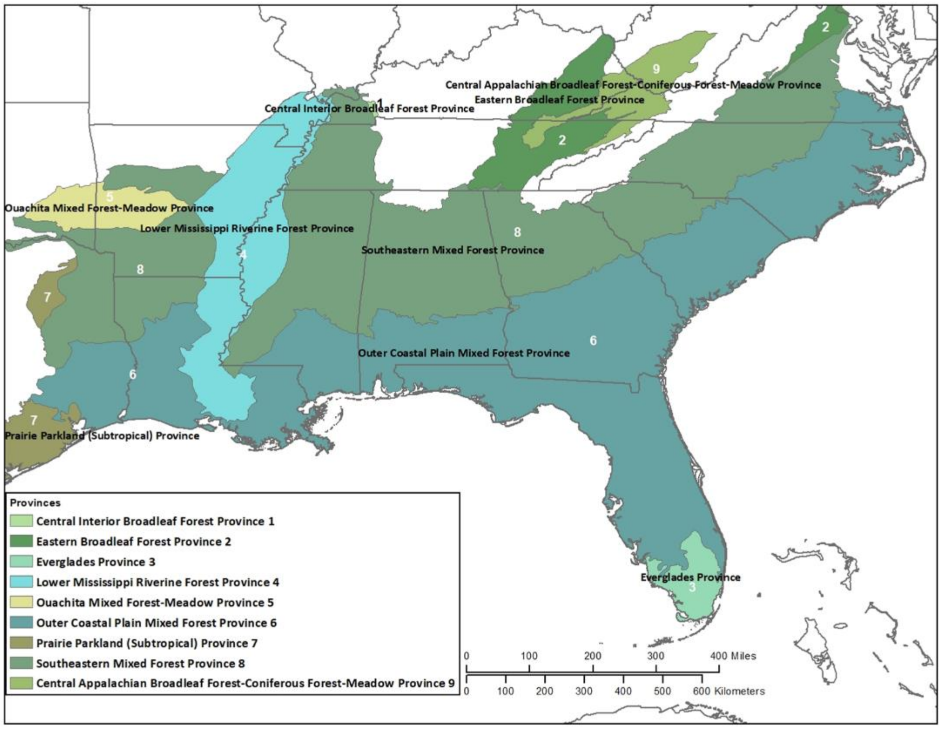


Figure 22. U.S. Forest Service ECOMAP.

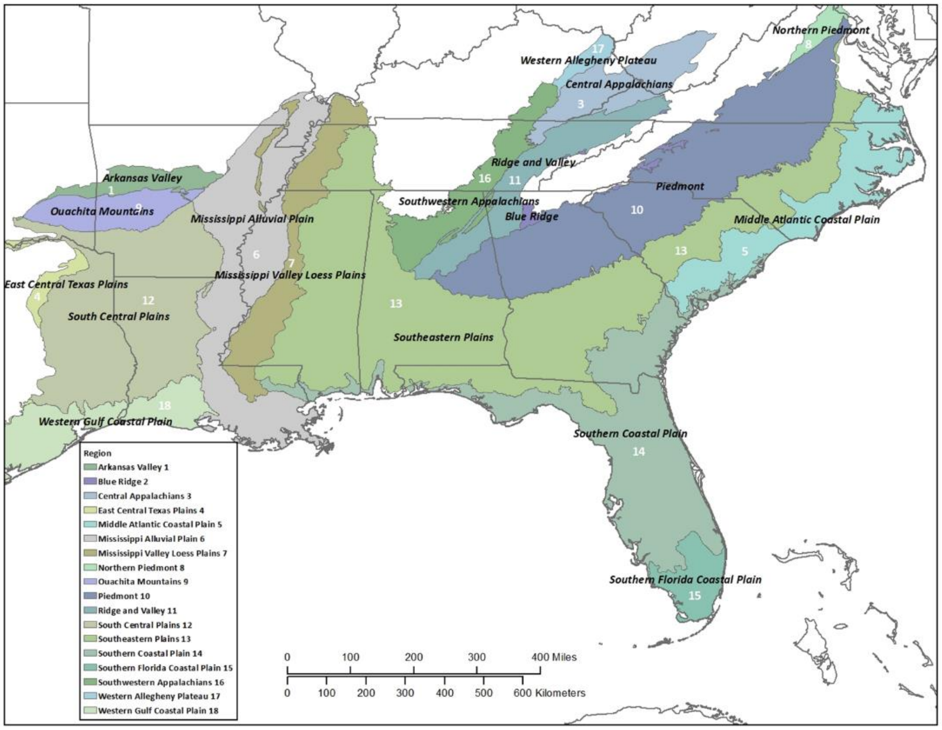


Figure 23. Environmental Protection Agency Level III ecoregions.

Ouachita Mountains Ecoregion

The Ouachita Mountains (Figure 20) are a distinctive northwestern-most RCW ecoregion of east-west trending mountains, hills and valleys. Fire-dependent shortleaf pine-bluestem communities were historically common and most dominant across the wide range of shortleaf pine in the Ouachita and Ozarks (Guldin et al. 1999), but declined significantly with timber harvesting in the early 20th century followed by fire suppression and land conversion (Hedrick et al. 2006). The southeastern pine savannas and woodlands described and coarsely mapped by Peet et al. (2018, Figure 8) did not include these shortleaf pine-bluestem communities because their subject was more focused on Coastal Plain and transitional types. Shortleaf pine-bluestem in the Ouachita Mountains, as characterized by the USNVC Ozark-Ouachita Shortleaf Pine-Oak Woodland Alliance, occurs on ridges and upper to middle slopes characteristically as an open pine-grassland community or woodland with widely scattered white oak (*Q. alba*), northern red oak (*Q. rubra*), and black oak (*Q. velutina*) above a well-developed herbaceous layer of little bluestem, slim-leaved panic grass (*Dicanthelium linearifolium*) and other grasses and forbs. Restoration of these communities on ridges and southern slopes over thin, rocky soils today is an important part of management in Ouachita National Forest (Hedrick et al. 2006) and as a broader initiative (Shortleaf Pine Initiative, http://shortleafpine.net/shortleaf-pine-initiative). The RCW in the Ouachita ecoregion is closely associated with the shortleaf pine-bluestem community. Major tracts of this woodland type occur in the Ouachita National Forest of Arkansas and the McCurtain County Wilderness Area of eastern Oklahoma. Climatically, the region has an average 52 inches rain per year, 3.5 inches of snow, an average temperature (F^o) of 61^o, an average daily January temperature of 38^o, and an average daily August temperature of 79^o.

Upper West Gulf Coastal Plain Ecoregion

The Upper West Gulf Coastal Plain (UWGCP) ecoregion encompasses parts of Arkansas, Oklahoma, Texas, and Louisiana (Figure 20). It is bordered by the Lower West Gulf Coast Plain to the south, the Gulf Coast Prairies and Marshes to the southeast, the Crosstimbers and Southern Tallgrass Prairie to the West, the Ouachita Mountains to the north, and the Mississippi River Alluvial Plain to the east. UWGCP elevations mostly are 150 – 300 feet above sea level across flats to rolling hills (ecoregion delineation between the Lower West Gulf Coastal Plain and the Upper West Gulf Coastal Plain is the northern limit of the longleaf pine terrestrial community. The region has an average 49 inches of rain per year, 0.6 inches of snow, an average temperature (F^o) of 64^o, an average January daily temperature of of 43^o, and an average daily August temperature of 81^o. May tends to be the wettest month with an average of 5.7 inches.

The UWGCP southern boundary corresponds closely with the northern historical range limit of longleaf pine west of the Mississippi River (Figure 8). The prevailing historical vegetation on most all UWGCP uplands was a fire-maintained upland pine and pine-hardwood forest on loamy to fine textured soils, dry to dry-mesic sites, with shortleaf pine and loblolly pine (TNC 2002).

Generally land use in the Upper West Gulf Coastal Plain has resulted in disturbance of various types and levels throughout the ecoregion. Many areas of biodiversity have experienced some kind of past disturbance including clearing for timber, agriculture, grazing, or mineral extraction. However, some of these areas have been, or are in the process of, being returned to a level of pre-settlement state. Unfortunately suppression of the natural fire regime has resulted in stressed or ecologically incomplete landscapes.

For purposes of recovery planning, the Upper West Gulf Coastal Plain Ecoregion contains one Primary Core population, the Sam Houston National Forest. Significant and important support populations include D'Arbonne National Wildlife Refuge, Felsenthal National Wildlife Refuge, Huntsville State Fish Hatchery, I.D. Fairchild State Forest, Upper Ouachita National Wildlife Refuge, and W.G. Jones State Forest. Recovery and management of RCW in this region has focused on restoration of suitable habitat for foraging and cavities through use of prescribed fire and other treatments to control understory and midstory hardwood encroachment, cavity management, and increasing populations with recruitment clusters and translocation of birds between populations.

West Gulf Coastal Plain Ecoregion

The West Gulf Coastal Plain ecoregion encompasses approximately 11.2 million acres (4,524,450 ha) or 17,469 square miles in eastern Texas and western Louisiana, extending from the western edge of the Mississippi River floodplain in Louisiana to the Trinity River in Texas, and from the prairies and marshes of the Gulf Coast north to the mixed pine-hardwood dominated rolling hills of northeast Texas and northern Louisiana. It is broadly defined as the area encompassing the natural range of longleaf pine dominated uplands on the Coastal Plain west of the Mississippi River.

The pre-settlement landscape was a mosaic of ecosystems, each responding to environmental gradients at various scales, such as regional climate and local patterns of soils, landform, and disturbance regimes. For example, the ecoregion is subject to periodic disturbances by hurricanes (roughly once per decade), and the frequency and intensity of disturbances are greatest in the southern portion of the ecoregion near the Gulf of Mexico. RCWs inhabit the upland longleaf pine, loblolly pine, and shortleaf pine forests in this ecoregion.

For purposes of recovery planning, the West Gulf Coastal Plain ecoregion contains 2 Primary Core populations (1) Angelina and Sabine National Forests and (2) Vernon Unit of the Calcasieu Ranger District of the Kistachie National Forest and Fort Polk; 2 Secondary Core populations (1) Davy Crockett National Forest and (2) Catahoula Ranger District/Winn Ranger District portions of the Kistachie National Forest; as well as several significant and important supporting populations. Recovery and management of RCWs in this region has focused on restoration of suitable habitat for foraging and cavities through use of prescribed fire and other treatments to control understory and midstory hardwood encroachment, cavity management, increasing populations with recruitment clusters and translocation, and conversion to longleaf pine at longleaf pine sites.

Upper East Gulf Coastal Plain Ecoregion

The Upper East Gulf Coastal Plain ecoregion encompasses 33,861,051 acres (13,703,081 ha) or 52,908 square miles. The region ranges from southern Illinois, western Kentucky and Tennessee, throughout much of Mississippi, east to Alabama and a limited area of Georgia, and southeastern Louisiana. The region is bounded on the west by the Mississippi River Alluvial Plain and on the north by the Ohio River, and Tennessee River (now Kentucky Lake).

The potential natural vegetation of the Upper East Gulf Coastal Plain may be characterized as broad bands of different composition that roughly parallel the coast. From south to north these include southern mixed forests, oak-hickory-pine forests, and oak-hickory forests, interrupted by occasional southern floodplain forests and black belt prairies (Küchler 1964). Southern mixed forests and oak-hickory-pine forests, the 2 predominant types in terms of area occupied, are recognized by the presence of longleaf pine and shortleaf pine respectively. Although longleaf forests and woodlands were the dominant vegetation type of the southeastern United States Coastal Plain, they occur in only limited areas of this region, extending landward into the Upper East Gulf Coastal Plain by only about 50 miles. Northward, longleaf pine is replaced by shortleaf pine.

Suppression of fire and inadequate fire regimes have impacted RCW populations, and have been exacerbated by intensive forest management. Although the establishment of pine plantations was not a widespread phenomenon in the region until the 1950’s, it has since impacted large areas and has become one of the most consequential forestry developments in the region in the last 35 years (McWilliams 1992). The total extent of natural habitat has been greatly reduced while remaining patches of habitat have become smaller and more isolated from one another and subjected to an increase in edge effects.

For purposes of recovery planning, the Upper East Gulf Coastal Plain ecoregion contains 1 Primary Core population (Bienville National Forest), 1 Secondary Core population (Oakmulgee Ranger District of the Talladega National Forest, and 1 Significant Support population (Noxubee National Wildlife Refuge). Recovery and management of RCWs in this region has focused on restoration of suitable habitat for foraging and cavities by increased use of prescribed fire and other treatments to control understory and midstory hardwood encroachment, cavity management, and increasing populations by recruitment clusters and translocation of birds between populations.

East Gulf Coastal Plain Ecoregion

The East Gulf Coastal Plain ecoregion encompasses portions of 5 states (Georgia, Florida, Alabama, Mississippi, and Louisiana) and over 42 million acres from the southwestern portion of Georgia across the Florida Panhandle and west to the southeastern portion of Louisiana. The ecoregion has a diversity of ecological systems, ranging from sandhills and rolling longleaf pine-dominated uplands to pine flatwoods and savannas, seepage bogs, bottomland hardwood forests, barrier islands and dune systems, and estuaries. RCWs inhabit the pineland ecosystem within this ecoregion, specifically areas of historic longleaf pine distribution.

The pineland ecosystem (consisting of fire-maintained longleaf pine and slash pine woodlands and their associated seepage bogs and depression wetlands) once dominated a string of ecoregions from southeastern Virginia to eastern Texas. This system has now been reduced to less than 5 percent of its former range, making it one of the most endangered landscapes in North America (Noss et al, 1995). Not only have these pineland ecosystems been directly reduced in extent, but remaining areas are also fragmented and many suffer from the exclusion of frequent fire, a critical ecological process for their maintenance and health.

For purposes of recovery planning, the Upper East Gulf Coastal Plain ecoregion contains 3 Primary Core populations (1) Central Florida Panhandle, consisting of Apalachicola and Wakulla Ranger Districts of the Apalachicola National Forest, Ochlockonee River State Park, St. Mark’s National Wildlife Refuge, and Tate’s Hell State Forest; (2) Chickasawhay Ranger District of the DeSoto National Forest, and (3) Eglin Air Force Base; and 3 Secondary Core populations (1) Conecuh/Blackwater, consisting of Conecuh National Forest and Blackwater River State Forest, (2) DeSoto Ranger District of the DeSoto National Forest, and (3) Homochitto National Forest. Recovery and management of RCWs in this region has focused on restoration of suitable habitat for foraging and cavities by increased use of prescribed fire and other treatments to control understory and midstory hardwood encroachment, cavity management, increasing populations by recruitment clusters and translocation of birds between populations, and conversion from off-site pines to longleaf pine.

South Atlantic Coastal Plain Ecoregion

The South Atlantic Coastal Plain ecoregion encompasses more than 23 million acres across 3 states, including the southern portion of South Carolina, southeastern Georgia and northeastern Florida. The ecoregion is bordered to the east by the Atlantic Ocean, and to the northwest by the Fall Line (a geologically distinct zone corresponding to the interface between the relatively flat coastal plain and the topographically varied Piedmont). It is bordered on the northeast by the Mid-Atlantic Coastal Plain, on the west by the East Gulf Coastal Plain, on the south by the Florida Peninsula and on the northwest the Sandhills. The many ecological systems found in the South Atlantic Coastal Plain ecoregion range from fall-line sandhills to rolling longleaf pine uplands to wet pine flatwoods; from small streams to large river systems to rich estuaries; from isolated depression wetlands to Carolina bays to the Okefenokee Swamp. Other ecological systems in the ecoregion include maritime forests on barrier islands, pitcher plant seepage bogs and Altamaha grit (sandstone) outcrops.

RCW inhabit the historic longleaf pine woodlands and associated ecological communities within this ecoregion. Longleaf pine woodlands and associated ecological communities were once the dominant vegetation type in this ecoregion. Fire-maintained longleaf pine woodlands are found across a wide range of soil moisture regimes, and support a large number of plant and animal species (including many endemics). Due to a drastic decline of longleaf pine woodlands across the South Atlantic Coastal Plain (less than 5 percent remains), many of these species are imperiled.

For purposes of recovery planning, the South Atlantic Coastal Plain Ecoregion contains 2 Primary Core populations: (1) Fort Stewart, and (2) Osceola/Okefenokee, consisting of Osceola National Forest and Okefenokee National Wildlife Refuge; a single Secondary Core population, the Savannah River Site; and several Significant and Important support populations (e.g. Charleston Naval Weapons Station, Persanti Island, Santee State Park, and Webb Wildlife Center). Recovery and management of RCW in this region has focused on re-establishment of suitable habitat for foraging and cavities, and the natural longleaf pine community through use of prescribed fire and other treatments to control understory and midstory hardwood encroachment, site conversion by longleaf pine planting, cavity management, and increasing populations with recruitment clusters and translocation of birds between populations.

South/Central Florida Ecoregion

The South/Central Florida ecoregion (hereafter Peninsula Florida) includes areas having a temperate flora and fauna characteristic of the Carolinian Biotic Province in its northern reaches, to species and communities with definite tropical affinities of the Caribbean Biotic Province at its southern limit (Myers and Ewel 1990). Encompassed by the Gulf of Mexico on its west and the Atlantic Ocean (and the Gulf Stream) on its east, the ecoregion includes hundreds of miles of coastline. The entire peninsula is characterized by relatively high rainfall, averaging 65 inches per year. The species and communities are shaped by several dominant forces: pronounced wet and dry seasons, once frequent fires that swept unimpeded for miles across the landscape and other large-scale disturbance factors like hurricanes, a high water table, mucky or peaty soils that have developed in numerous depressional features on a karst, limestone-based substrate, a relatively flat terrain where even slight changes in topography can dramatically influence the kind of community that develops, and generally infertile, moderately to excessively well-drained sandy soils on several prominent ridge systems that run parallel to the coastlines (Myers and Ewel 1990).

RCWs occupy pine forests in both upland and lowland areas within the Florida Peninsula. Upland areas in the northern portion of the ecoregion, include several ridges comprised of deep, Pleistocene-deposited sands parallel to the coasts, the Brooksville Ridge on the upper west coast and the Trail Ridge and Crescent City Ridges on the east coast. All of these sandy ridge systems have the longleaf pine dominated sandhill ecological system (one of three matrix ecological communities/systems in the ecoregion) as their primary vegetational feature. Areas of lower topography than the ridge systems, but not low enough to sustain marsh or swamp vegetation, include flatwoods – a matrix community characterized by a pine canopy of either longleaf pine or slash pine depending upon the soils and location within the range of these species, , a thick, low shrub stratum and a highly diverse ground cover vegetation.

For purposes of recovery planning, the Florida Peninsula ecoregion is 1 of 2 recovery units that do not contain a primary or secondary population. However, maintaining populations of RCWs in south and central Florida is essential to the recovery of the species. These populations are associated with unique habitat types such as native hydric slash pine (Beever and Dryden 1992) and critically endangered sand ridge communities. In addition, south and central Florida served as the source of the longleaf pine/scrub oak community roughly 5000 to 8000 years ago (Watts 1971, Watts et al. 1992). The region was a refuge for RCWs during the Wisconsin Glaciation just prior to the longleaf advance, and it is likely that RCW evolved here during a previous glacial event (Jackson 1971, Conner et al. 2001a). Therefore, RCWs in south and central Florida are considered an essential component of the species.

Essential Support populations within the Florida Peninsula include: (1) Avon Park, consisting of Avon Park Air Force Range and Kicco Wildlife Management Area, (2) Babcock/Webb Wildlife Management Area, (3) Big Cypress National Preserve, (4) Camp Blanding Training Site, (5) Goethe State Forest, (6) Hal Scott Preserve, (7) Corbett/Dupuis, consisting of J. W. Corbett Wildlife Management Area and Dupuis Wildlife Management Area, (8) Ocala National Forest, (9) Picayune Strand State Forest, (10) St. Sebastian River State Buffer Preserve, (11) Three Lakes Wildlife Management Area, (12) Withlacoochee State Forest – Citrus Tract, and (13) Withlacoochee State Forest – Croom Tract. Management in this region has focused on increased use of prescribed fire and other treatments to control understory and midstory hardwood encroachment to restore suitable habitat, cavity management, and increasing population size particularly by translocation of birds between populations.

Piedmont Ecoregion

The Piedmont ecoregion stretches from south-central Maryland to east-central Alabama over 680 miles through portions of 6 states (Alabama, Georgia, South and North Carolina, Virginia, & Maryland) and covers 42,343,801 acres (17,135,928 ha). The Piedmont or foothills of the Appalachian Mountains is the oldest and most eroded part of the original Appalachian orogeny. It is bounded by the Coastal Plain to the east and the Southern Appalachians to the west. Elevations range from approximately 600 to 1,500 feet. Rolling hills with broad ridges that are irregularly and frequently dissected by drainages are typical of the Piedmont.

Oak-hickory forest is a widely distributed community that varies from site to site, with pine-hardwood and hardwood-pine communities on ridges and dry sites. Occurring in highly fragmented stands, later successional stages tend to be made up of a diverse assemblage of hardwoods, primarily oaks and hickories, as co-dominants in combination with pines. Understory, shrub and herbaceous layers are present in varying degrees, represented by diverse woody and non-woody species. Vegetation on most sites consists of early- to mid-successional managed stands of pine and pine-hardwood forest. The understory in pure pine stands is often open, but in mixed or older stands, it is dominated by the hardwoods characteristic of the site. Common pine species of the Piedmont include shortleaf and loblolly, with the former better adapted to dry, fine textured upland soils and loblolly achieving maximum growth on deep soils with good moisture and drainage.

The Piedmont has undergone many human-induced changes over the past few centuries. Extensive, open oak-hickory-pine forests with isolated prairies and grasslands are believed to have occupied the vast majority of the region; hence they are considered the ecological ‘matrix’ vegetation across the bulk of the ecoregion. Tornadoes, ice storms and hurricanes, droughts and floods, lightening and anthropogenic fires have shaped and disturbed these forests. These forests have been heavily worked prior to and since the arrival of European settlers. Native Americans cleared forests for agriculture and the Europeans continued to clear large tracts of forestland for agriculture, home sites, forest industry, and other uses.

For purposes of recovery planning, the Piedmont ecoregion contains 1 Secondary Core population: Oconee/Piedmont, consisting of Oconee National Forest and Piedmont National Wildlife Refuge. Recovery and management of RCWs in this region has focused on restoration of suitable habitat, with cavity management, through prescribed fire, thinning, and other treatments, with recruitment clusters to increase populations.

Sandhills Ecoregion

The Sandhills are an inland habitat type, characterized by rolling hills capped by deep coarse sands. They are wedged between the Coastal Plain and Piedmont regions of North and South

Carolina and Georgia. Because the Sandhills contain dry, nutrient-poor soil, this habitat contains only plants adapted to such harsh conditions. The biodiversity of the Sandhills depends on a combination of relatively high rainfall, very porous, sandy soils and frequent fire that creates a mosaic of longleaf pine community types. Longleaf pine is the dominant tree species in this system and is essential to its integrity, but the floral and faunal diversity of the system lies in the forest understory. In fact, the longleaf pine–wiregrass forest may well be the most diverse North American ecosystem north of the tropics, containing rare plants and animals not found anywhere else.

The history and current status of human activities in the Sandhills has greatly reduced longleaf pine habitat. Interruption of natural fire regimes in the Southeast has resulted in alteration of native plant abundance to a degree that threatens long-term longleaf pine ecosystem sustainability. The decline of longleaf pine, native grasses and forbs and increase in competing trees and shrubs, forming high-density midstory fuel ladders, are the direct results of decreased fire frequencies. These altered ecosystems have become increasingly vulnerable to destruction by catastrophic fire, which may also directly threaten human life and property, and invasion by noxious weeds and undesirable woody plants.

For purposes of recovery planning, the Sandhills ecoregion contains 2 Primary Core populations: (1) North Carolina Sandhills East, consisting of the Calloway Tract (owned by The Nature Conservancy), Carver's Creek Tract, Fort Bragg, McCain Tract, and Weymouth Woods Sandhills Nature Preserve; and (2) Fort Benning; 1 Secondary Core population: the South Carolina Sandhills, consisting of Carolina Sandhills National Wildlife Refuge and Sand Hills State Forest; and 1 Essential Support population: North Carolina Sandhills West, consisting of Camp Mackall and the Sandhills Game Lands. There are many Important and Significant populations including Cheraw State Fish Hatchery, Cheraw State Park, Fort Gordon, Fort Jackson, Manchester State Forest, and Poinsett Weapons Range. Recovery and management of RCWs in this region has focused on restoration of the natural longleaf pine community to provide suitable habitat through use of prescribed fire and other treatments to control understory and midstory hardwood encroachment, cavity management, conversion to longleaf pine, and increasing populations with recruitment clusters and translocation of birds between populations.

Mid-Atlantic Coastal Plain Ecoregion

The Mid-Atlantic Coastal Plain occupies 26 million acres east of the fall line between the Piedmont and Atlantic Coastal Plain, south of the James River in Virginia and north of Charleston Harbor in South Carolina. About two-thirds of this ecoregion is in North Carolina. Longleaf pine historically dominated the uplands, reaching the northern limit of this species in southeastern Virginia. The Mid-Atlantic Coastal Plain was the site of the first successful European settlement in North America. The natural landscape has been altered by European culture for nearly 4 centuries. By 1790, the region supported more than 600,000 people. In the intervening 200 years, the human population has grown to more than 10.5 million. Currently, the urban crescent from Baltimore south to Richmond and east to Norfolk is one of the fastest growing regions in North America. Growth is expected to continue into the foreseeable future, placing increasing demands on the region's natural resources. The development of modern silvicultural practices in the 1950s and 1960s and their widespread use over the past 60 years has led to a dramatic shift in forest structure and distribution.

For purposes of recovery planning, the Mid-Atlantic Coastal Plain Ecoregion contains 2 Primary Core populations: (1) Coastal North Carolina, consisting of Croatan National Forest, Holly Shelter Game Lands, and Marine Corps Base Camp Lejeune (2) Francis Marion National Forest; 1 Essential Support population: Northeast North Carolina/Southeast Virginia, consisting of Alligator River National Wildlife Refuge, Dare County Bombing Range, Palmetto-Peartree Preserve (owned by North Carolina Wildlife Resources Commission), Pocosin Lakes National Wildlife Refuge, and Piney Grove Preserve (owned by The Nature Conservancy). The ecoregion also has many Important and Significant Support populations including Bladen Lakes State Forest, Hampton Plantation State Park, Jones Lake State Park, Lewis Ocean Bay Heritage Preserve, Longleaf Pine Heritage Preserve, Military Ocean Terminal Point Sunny Point, Sandy Island, Santee Coastal Reserve, Bonneau Ferry WMA, Singletary Lake State Park, Wedge Plantation, and Yawkey Wildlife Center. Recovery and management of RCWs in this region has focused on restoration of suitable habitat with prescribed fire, thinning, and other treatments to control understory and midstory hardwood encroachment, conversion to longleaf pine, cavity management, and increasing populations with recruitment clusters and translocation of birds between populations.

Redundancy

For the RCW to maintain viability, the species also needs to exhibit some degree of redundancy. Species-level redundancy reflects the ability of a species to withstand catastrophic events, and is best achieved by having multiple, widely distributed populations relative to the spatial occurrence of catastrophic events. In addition to guarding against a single or series of catastrophic events, redundancy is important to protect against losing irreplaceable sources of adaptive diversity. Having multiple populations distributed across the range of the species and within representative units, will help preserve the breadth of adaptive diversity, and hence, the evolutionary flexibility of the species. Thus, RCW redundancy is described as having multiple, resilient populations widely distributed across the breadth of adaptive diversity relative to the spatial occurrence of catastrophic events.

An important question when investigating redundancy for RCW is, "what exactly is a catastrophe?" We consider a catastrophe to be any population level impact that has the potential to negatively influence population resiliency outside of normal environmental and demographic stochasticity. Catastrophic events may be acute or chronic. Thus, catastrophic natural impacts are not limited to acute effects that cause extirpation instantaneously or nearly so over very short time intervals. Chronic impacts from infrequent but recurring ice-storms, tornados, tropical depressions and hurricanes, pine beetles, or other factors may incrementally increase mortality, reduce productivity, and reduce the number of active territories at magnitudes to significantly decrease resilience. Because of the extreme management dependence of RCWs, the ability of a population to "bounce back" from acute and chronic catastrophic events is highly influenced by the management response following a catastrophe. For example, hurricanes represent a potential catastrophic event, particularly for populations near the coast. There are many examples of hurricanes impacting RCW populations, and focused management responses (e.g. replacement of artificial cavities, post-storm mid-story control, and hazardous fuel reduction) ameliorated over time much of the population level impacts from these storm events. It is important to note that without deliberate post-hurricane management and similar responses to other events, some populations likely would not have recovered to pre-storm conditions and could have been extirpated or driven to more vulnerable condition.

In summary, a species needs a suitable combination of all 3 characteristics (resilience, representation, and redundancy) for long-term viability. While RCWs exhibit some degree of each of these characters, the amount appears greatly reduced over historical levels, and currently largely maintained by intensive human management intervention.

CHAPTER 4: CURRENT CONDITION

Below we assess current resilience, representation, and redundancy as they relate to population and habitat factors known to be important for species viability. The key to assessing current condition for RCW is investigating past trends in abundance and growth rates. Underlying these past trends are management and stochastic factors discussed in the previous section (e.g. cavity management, prescribed fire, hurricanes).

Current Population Resilience

Resiliency describes the ability of populations to withstand deterministic and low-level stochastic events (arising from random factors). Highly resilient populations are better able to withstand disturbances such as random fluctuations in birth rates (demographic stochasticity), annual variation in rainfall (environmental stochasticity), or the effects of anthropogenic activities.

We measured resiliency at the population level for this assessment, primarily by evaluating the current population size as number of active clusters and secondarily by the associated past growth rate. Populations are located on properties owned by a variety of agencies and private entities including but not limited to the Department of Defense, U.S. Forest Service, state wildlife and natural resource agencies, Department of Energy, state forest service, U.S. Fish and Wildlife Service, and a variety of private landowners. The data used to calculate number of current active clusters and population growth rates came from a variety of sources, and in some cases we had to make some assumptions depending on the data resolution. The breadth of data sources and the corresponding decisions made based on the data resolution are detailed below.

Values for current numbers of active clusters were derived from the most recent estimates we were able to obtain. In most cases, these estimates were available from the Service's Annual RCW Property Data Report database and represented the total number of active clusters during the 2016 breeding season. When possible, we obtained updated numbers for the 2017 breeding season from GIS files or other sources. For a few populations, we were not able to obtain population size estimates as recent as 2016, so we used the most current population size we were able to obtain. No current population size estimates are older than the 2013 breeding season.

To calculate growth rates for a given demographic population we obtained past time series abundance data for annual number of active clusters for as long as possible, not to precede 1998. We did not seek or use data prior 1998 for several reasons. Abundance and spatial data are not available prior to 1998 for most demographically delineated populations. The best available data for most populations is for 1998 and afterwards concurrent with the implementation of the Service's Annual RCW Property Data Report database. Also, as discussed in previous sections, the management paradigm for RCWs changed dramatically in the late 1990s (e.g. cavity management, recruitment clusters) to sustain and increase populations, and we wanted to capture the results of this new and more effective management. It is important to note that much of our abundance data is limited to a property level. Thus, if a property has multiple current demographic populations, we often lacked a past and spatially explicit time series for those individual demographic populations. In these cases, we calculated a "property level" population growth rate, and applied it to all of the demographic populations occurring on that property.

Currently, there are at least 124 demographic populations across the range of the RCW (Table 3). Although we have not categorized overall resilience, we have categorized two important parameters related to population resiliency: current population size and associated population growth rate. Population size categories are as follows: very low (<30 active clusters); low (30-99 active clusters); moderate (100-249 active clusters); high (250-499 active clusters); and very high (>500 active clusters). This categorization is based largely on modeling of the dynamics of idealized RCW populations by Walters et al. (2002b) as validated by Schiegg et al. (2005) and Walters et al. (2011). Walters et al. (2002b) employed a spatially-explicit, individual-based RCW model that incorporated demographic and environmental stochasticity, and thus is appropriate for assessing resilience. In subsequent applications, the demographic effects of inbreeding depression on population size and persistence were added (Daniels et al. 2000, Schiegg et al. 2006) based on empirical RCW data of inbreeding effects. In their analysis, populations were modeled with unlimited, high quality foraging and nesting habitat, with sufficient and well distributed old pines for natural cavity excavation, but were not subject to management techniques designed to stimulate population growth (e.g., recruitment clusters and cavity management). Population growth was limited to pioneering and budding with natural cavity excavation. Population growth, persistence, risks of extirpation and other output of these model simulations provides a template to identify inherent population resilience against results of the relative success or failure of management for this conservation-reliant species.

Under these model and simulation conditions, populations of 25 (our very low category) and 50 (low) active clusters always declined in response to spatial aggregation, density of groups, and inbreeding depression. Simulated populations of 250 (high) and 500 (very high) were stable on average regardless of spatial aggregation and density at comparative densities to the spatially delineated demographic SSA populations, although the smaller populations near 250 in this size-class could have a declining growth rate slightly less than 1.0. Populations of 100 to 250 groups were stable at high levels of aggregation and density, but declining at lower levels. Thus our moderate category captures the range within which stability was dependent on spatial aggregation and density of groups. We used 30 active clusters rather than 25 as our boundary between the very low and low categories because 30 is a threshold for differences in management in the species' Recovery Plan (USFWS 2003), particularly for RCW translocation management benefits, as well as a threshold for differences in population behavior observed in our global model analysis.

When we had at least 5 years of past abundance data we estimated a population growth rate by comparing the initial population size to the final population size and calculating the rate of growth required to produce the observed change in population size. Thus the figures we present are constant growth rates. Based on these rates we categorized populations as decreasing ($\lambda < 1$), increasing ($\lambda > 1.02$) or stable ($\lambda = 1.00\text{-}1.02$).

Our primary categorization of current resilience is based on population size. We use population growth rate as a secondary factor to indicate relative resilience of populations within each of the five resilience categories (see below). Of the 124 populations analyzed, we classified the resilience of 3 populations as very high; 3 as high; 10 as moderate; 37 as low; and 71 as very low (Table 3). In any category, management has been essential to restore and sustain foraging habitat with prescribed fire, silviculture and other treatments, and provide sufficient cavities.

Table 3. Current baseline resilience condition (Current Baseline Category) for RCW populations by ecoregion, including population size and associated growth rates. UA: data not available, n/a: not applicable due to missing data, and *: growth rates for the demographic population were computed and estimated in the absence of demographic population data according to abundance for all RCWs at the entire property level across multiple demographic populations. Populations are listed by descending current population size (Current Pop Size).

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest	858	Very High	2016	662	2000	1.016	Stable	EGCP
North Carolina Sandhills	781	Very High	2016	775	2014	n/a	n/a	SH
Eglin Air Force Base	504	Very High	2015	308	2001	1.036	Increasing	EGCP
Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA	496	High	2014	354	1998	1.021	Increasing	MACP
Fort Stewart	482	High	2016	189	1998	1.053	Increasing	SACP
Fort Benning	386	High	2016	256	1998	1.023	Increasing	SH
Carolina Sandhills NWR-Sandhills State Forest-Cheraw State Park	248	Moderate	2015	182	1998	1.018	Stable	SH
Fort Polk-Vernon Unit Kisatchie National Forest	223	Moderate	2015	190	1999	1.010	Stable	WGCP
Sam Houston National Forest A	158	Moderate	2016	70	2005	1.077	Increasing	UWGCP
Evangeline Unit Kisatchie National Forest-Alexander	152	Moderate	2015	119	2005	1.025	Increasing	WGCP
Osceola National Forest	152	Moderate	2016	63	2000	1.057	Increasing	SACP
Homochitto National Forest	151	Moderate	2017	UA	UA	n/a	n/a	EGCP
Blackwater River State Forest E-Conecuh National Forest A	138	Moderate	2016	105	2012	n/a	n/a	EGCP
Bienville National Forest A	117	Moderate	2015	106*	1998*	1.020	Stable	UEGCP
Oakmulgee District A Talladega National Forest	114	Moderate	2016	87	2003	1.021	Increasing	UEGCP
Palmetto-Peartree Preserve Complex	102	Moderate	2016	UA	UA	n/a	n/a	MACP
Georgia Safe Harbor	97	Low	2016	UA	UA	n/a	n/a	EGCP
Marine Corps Base Camp Lejeune B	91	Low	2016	41	1998	1.045	Increasing	MACP
Brosnan Forest	86	Low	2015	67	1998	1.015	Stable	SACP
Big Cypress National Preserve A	83	Low	2016	62	2009	1.043	Increasing	FP
Piedmont NWR-Oconee National Forest-Hitchiti Experimental Forest	83	Low	2016	53	1998	1.025	Increasing	P
Withlacoochee State Forest Citrus	82	Low	2016	50	1998	1.028	Increasing	FP
Ouachita National Forest A	71	Low	2016	50	2009	1.051	Increasing	OM
Chickasawhay District DeSoto National Forest	69	Low	2016	47	2012	n/a	n/a	EGCP
Croatan National Forest	69	Low	2013	59	1999	1.011	Stable	MACP
Sam Houston National Forest B	67	Low	2016	47	2005	1.033	Increasing	UWGCP
Davy Crockett National Forest A	59	Low	2017	63	2012	0.987	Decreasing	UWGCP
Ocala National Forest A	58	Low	2016	7	1998	1.125	Increasing	FP
Catahoula B Kisatchie National Forest	57	Low	2016	60	2014	n/a	n/a	WGCP
Savannah River Site A	57	Low	2016	17	1998	1.070	Increasing	MACP
DeSoto District DeSoto National Forest B	53	Low	2017	25	2007	1.078	Increasing	EGCP
Angelina National Forest C	51	Low	2016	32	2010	1.081	Increasing	WGCP
DeSoto District DeSoto National Forest A	47	Low	2017	47	2016	n/a	n/a	EGCP
Sandy Island	46	Low	2015	36	1998	1.015	Stable	MACP
Three Lakes WMA	45	Low	2016	50	2000	0.993	Decreasing	FP
Goethe State Forest B	44	Low	2016	13	1998	1.070	Increasing	FP
Kisatchie District Kisatchie National Forest C-Peason	42	Low	2015	43	2003	0.998	Decreasing	WGCP
Babcock Webb WMA	41	Low	2015	27	1998	1.025	Increasing	FP
Fort Jackson	41	Low	2016	13	1998	1.066	Increasing	SH

Table 3. Continued.

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Ocala National Forest C	40	Low	2016	5	1998	1.122	Increasing	FP
Withlacoochee State Forest Croom	39	Low	2016	6	1998	1.110	Increasing	FP
Kisatchie District Kisatchie National Forest A	38	Low	2016	53	1998	0.982	Decreasing	WGCP
Holly Shelter Game Land	36	Low	2016	38	1999	0.997	Decreasing	MACP
Avon Park Air Force Range	35	Low	2016	21	2000	1.032	Increasing	FP
Felsenthal-TNC	35	Low	2016	28	2000	1.014	Stable	UWGCP
Sam Houston National Forest F	35	Low	2016	20	2005	1.052	Increasing	UWGCP
Savannah River Site B	35	Low	2016	12	1998	1.061	Increasing	SACP
Marine Corps Base Camp Lejeune A	33	Low	2016	7	1998	1.090	Increasing	MACP
Jones Ecological Research Center	32	Low	2015	2	1996	1.157	Increasing	EGCP
Manchester Poinsett	32	Low	2015	10	1998	1.071	Increasing	SH
Sabine National Forest A	32	Low	2016	19	2010	1.091	Increasing	UWGCP
Camp Blanding	31	Low	2016	24	2005	1.024	Increasing	SACP
Silver Lake WMA	31	Low	2016	3	1998	1.139	Increasing	EGCP
Sam D. Hamilton Noxubee NWR B	28	Very Low	2016	29	2007	0.996	Decreasing	UEGCP
Bienville National Forest B	25	Very Low	2015	106*	1998*	1.020	Increasing	UEGCP
Conecuh National Forest B	25	Very Low	2016	9	1998	1.058	Increasing	EGCP
Davy Crockett National Forest B	25	Very Low	2017	12	2002	1.050	Increasing	WGCP
Fort Gordon	24	Very Low	2015	2	1998	1.157	Increasing	SH
Northeast North Carolina B	24	Very Low	2016	UA	UA	n/a	n/a	MACP
Shoal Creek District-Talladega National Forest	23	Very Low	2015	2	1998	1.155	Increasing	CSRV
Corbett Private Land	22	Very Low		UA	UA	n/a	n/a	MACP
Goethe State Forest A	22	Very Low	2016	17	1998	1.014	Stable	FP
Sabine National Forest B	22	Very Low	2016	14	2010	1.078	Increasing	WGCP
Crowell Lumber	21	Very Low	2015	21	2011	n/a	n/a	WGCP
Winn District Kisatchie National Forest A	21	Very Low	2017	20	2013	n/a	n/a	WGCP
Winn District Kisatchie National Forest B	21	Very Low	2017	4	2002	1.117	Increasing	WGCP
Big Branch Marsh NWR	20	Very Low	2016	15	2000	1.018	Stable	GCPM
Hal Scott-Stanton	20	Very Low	2016	13	1999	1.026	Increasing	FP
Ocala National Forest B	20	Very Low	2016	5	1998	1.080	Increasing	FP
Military Ocean Terminal Supply Point	19	Very Low	2015	6	1998	1.070	Increasing	MACP
Northeast North Carolina C	19	Very Low	2016	UA	UA	n/a	n/a	MACP
Bull Creek Triple N WMA	18	Very Low	2016	7	2003	1.075	Increasing	FP
Corbett WMA	17	Very Low	2014	12	1998	1.022	Increasing	FP
Angelina National Forest A	16	Very Low	2016	9	2004	1.049	Increasing	WGCP
Dupuis Wildlife and Environmental Area	16	Very Low	2015	3	2007	1.233	Increasing	FP
Okefenokee NWR B	15	Very Low	2015	12	2008	1.032	Increasing	SACP
Sam Houston National Forest D	15	Very Low	2016	7	2005	1.072	Increasing	UWGCP
Yawkey Wildlife Center	15	Very Low	2015	7	1998	1.046	Increasing	MACP
McCurtain County Wilderness Area	14	Very Low	2015	11	1998	1.014	Stable	OM
Piney Grove	14	Very Low	2016	3	1999	1.095	Increasing	MACP
Talladega	14	Very Low	2015	3	2009	1.293	Increasing	CSRV
Webb Wildlife Center	14	Very Low	2015	10	1998	1.020	Stable	SACP
Okefenokee NWR D	13	Very Low	2015	9	2008	1.054	Increasing	SACP
Picayune Strand State Forest B	13	Very Low	2016	3	1999	1.090	Increasing	FP
St. Sebastian River Preserve State Park	13	Very Low	2016	9	1999	1.022	Increasing	FP
Warren Prairie Natural Area	13	Very Low	2016	4	2000	1.076	Increasing	UWGCP
Babcock Ranch Preserve	12	Very Low	2017	10	2012	1.037	Increasing	FP
Catahoula A Kisatchie National Forest-Winn Kisatchie National Forest	12	Very Low	2016	7	2002	1.039	Increasing	WGCP
Lewis Ocean Bay Heritage Preserve	11	Very Low	2015	4	1998	1.061	Increasing	MACP

Table 3. Continued.

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Okefenokee NWR A	11	Very Low	2015	2	1998	1.105	Increasing	SACP
Bienville National Forest C	10	Very Low	2015	106*	1998*	1.020	Stable	UEGCP
Mitchell Lake	10	Very Low	2017	UA	UA	n/a	n/a	P
Okefenokee NWR C	9	Very Low	2015	6	2008	1.060	Increasing	SACP
TNC Disney Wilderness Preserve	9	Very Low	2016	4	2008	1.107	Increasing	FP
Longleaf Heritage Preserve - Lynchburg Savanna Heritage Preserve WMA	8	Very Low	2015	6	2012	n/a	n/a	MACP
Sabine National Forest C	7	Very Low	2016	3	2010	1.152	Increasing	WGCP
Angelina National Forest B	6	Very Low	2016	6	2010	1.000	Stable	WGCP
Catahoula C Kisatchie National Forest	6	Very Low	2016	7	1998	0.991	Decreasing	WGCP
Platt Branch Wildlife and Environmental Area	6	Very Low	2016	5	2004	1.015	Stable	FP
St. Marks NWR B	6	Very Low	2017	3	2016	n/a	n/a	EGCP
Big Cypress National Preserve B	5	Very Low	2016	3	2007	1.058	Increasing	FP
Kisatchie District Kisatchie National Forest B	5	Very Low	2016	5	1998	1.000	Stable	WGCP
Oakmulgee District B Talladega National Forest	5	Very Low	2016	6	2003	0.986	Decreasing	UEGCP
Ouachita National Forest B	5	Very Low	2016	1	2009	1.258	Increasing	OM
Picayune Strand State Forest A	5	Very Low	2016	1	2008	1.223	Increasing	FP
Jones State Forest	4	Very Low	2017	UA	UA	n/a	n/a	UWGCP
Northeast North Carolina D	4	Very Low	2016	UA	UA	n/a	n/a	MACP
Sam Houston National Forest C	4	Very Low	2016	3	2005	1.333	Increasing	UWGCP
D’Arbonne NWR	3	Very Low	2016	4	1999	0.983	Decreasing	UWGCP
Pine City Natural Area	3	Very Low	2016	1	1998	1.063	Stable	MRAP
Sam D. Hamilton Noxubee NWR A	3	Very Low	2016	9	2007	0.885	Decreasing	UEGCP
Sam Houston National Forest E	3	Very Low	2016	3	2005	1.000	Stable	UWGCP
Fairchild State Forest	2	Very Low	2017	UA	UA	n/a	n/a	UWGCP
Georgia Safe Harbor B	2	Very Low	2016	UA	UA	n/a	n/a	EGCP
Georgia Safe Harbor C	2	Very Low	2016	UA	UA	n/a	n/a	EGCP
Persanti Island	2	Very Low	2016	3	1998	0.978	Decreasing	MACP
Felsenthal NWR	1	Very Low	2016	UA	UA	n/a	n/a	UWGCP
Holly Shelter Game Land B	1	Very Low	2016	2	1999	0.960	Decreasing	MACP
Holly Shelter Game Land C	1	Very Low	2016	2	2000	0.958	Decreasing	MACP
Northeast North Carolina E	1	Very Low	2016	UA	UA	n/a	n/a	MACP
Northeast North Carolina F	1	Very Low	2016	UA	UA	n/a	n/a	MACP
Northeast North Carolina G	1	Very Low	2016	UA	UA	n/a	n/a	MACP
Northeast North Carolina H	1	Very Low	2016	UA	UA	n/a	n/a	MACP
Upper Ouachita NWR	1	Very Low	2016	1	1998	1.000	Stable	UWGCP

Figure 24. Current demographically delineated populations by current resilience category. Number of active clusters labelled for each population.

Except in rare instances, the vast majority of these populations currently remain dependent on the provision of artificial cavities until forest conditions mature to provide older pines for natural cavity excavation. Many of these small populations with less than 30 PBGs have been recipients of translocated RCWs to augment population size and growth. Also, recruitment clusters have been widely used to increase populations. Thus, most of the current populations have benefitted from various conservation management actions to sustain or increase populations.

Although we did not explicitly factor growth rate into our primary resilience classification scheme, growth rates reflect relative effectiveness of conservation management and population performance. Growth rates may be a consequence of how a population is being managed, the suitability of the location for the species, or a combination of these and other factors. Thus, past population performance may be indicative of future population performance to the extent that past dependence on conservation management actions continues in the future. Associated constant growth rates for each population in each resilience category are in Table 3. To summarize, 13 populations have decreasing growth rates, 66 are increasing, 19 are stable, and 26 could not be assessed (Table 4).

Table 4. Current condition for RCW populations by resilience category and growth rate. Total number of populations does not match Table 3 because sufficient data were not available to calculate growth rates for all populations.

Growth Rate	Baseline Resilience Class					
	Very Low	Low	Moderate	High	Very High	Total
Decreasing	8	5	0	0	0	13
Stable	11	4	3	0	1	19
Increasing	34	24	4	3	1	66
Total	53	33	7	3	2	98

Resilience: Very High

Table 5 summarizes all populations that are classified as “very high” for current resilience, rank order based on growth rate. The North Carolina Sandhills population did not have sufficient past data for a minimum of 5 years to calculate a constant growth because this population was formed by a recent demographic merger in 2016 of several disconnected populations managed by a variety of agencies and private entities. Although the Apalachicola National Forest-St. Marks-Tate’s Hell population is the current largest, the Eglin Air Force Base population has been growing at a higher annual rate (λ = 1.036), highlighting high population performance.

Table 5. Population resilience summary for “very high” category sorted by descending lambda (λ). n/a: not applicable due to missing data.

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Eglin Air Force Base	504	Very High	2015	308	2001	1.036	Increasing	EGCP
Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest	858	Very High	2016	662	2000	1.016	Stable	EGCP
North Carolina Sandhills	781	Very High	2016	775	2014	n/a	n/a	SH

Resilience: High

Table 6 summarizes all populations that are classified as “high” for current resilience, rank order based on growth rate. All populations within this resilience category have an increasing growth rate, showing high population performance. Fort Stewart in particular shows excellent population performance with annual growth exceeding 5%.

Table 6. Population resilience summary for “high” category sorted by descending lambda (λ).

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Fort Stewart	482	High	2016	189	1998	1.053	Increasing	SACP
Fort Benning	386	High	2016	256	1998	1.023	Increasing	SH
Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA	496	High	2014	354	1998	1.021	Increasing	MACP

Resilience: Moderate

Table 7 summarizes all populations that are classified as “moderate” for current resilience, rank order based on growth rate. Population sizes in the moderate category range from 102-248 active clusters, and consist of both stable and increasing populations. The moderate category is a transitional resilience category in that these populations, unlike those in the high and very high categories, may vary considerably in their resilience depending on population size, management and the spatial distribution and density of active clusters. The Sam Houston National Forest A and Osceola National Forest have been increasing at >5% annually, showing excellent population performance and the capability to be categorized as “high” resilience in the near future.

Table 7**.** Population resilience summary for "moderate" category sorted by descending lambda (λ). UA: data not available, n/a: not applicable due to missing data, and *: growth rates for the demographic population were computed and estimated in the absence of demographic population data according to abundance for all RCWs at the entire property level across multiple demographic populations.

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Sam Houston National Forest A	158	Moderate	2016	70	2005	1.077	Increasing	UWGCP
Osceola National Forest	152	Moderate	2016	63	2000	1.057	Increasing	SACP
Evangeline Unit Kisatchie National Forest-Alexander State Forest	152	Moderate	2015	119	2005	1.025	Increasing	WGCP
Oakmulgee District A Talladega National Forest	114	Moderate	2016	87	2003	1.021	Increasing	UEGCP
Bienville National Forest A	117	Moderate	2015	106*	1998*	1.020	Stable	UEGCP
Carolina Sandhills NWR-Sandhills State Forest-Cheraw State Park	248	Moderate	2015	182	1998	1.018	Stable	SH
Fort Polk-Vernon Unit Kisatchie National Forest	223	Moderate	2015	190	1999	1.010	Stable	WGCP
Homochitto National Forest	151	Moderate	2017	UA	UA	n/a	n/a	EGCP
Blackwater River State Forest E-Conecuh National Forest A	138	Moderate	2016	105	2012	n/a	n/a	EGCP
Northeast North Carolina A	102	Moderate	2016	UA	UA	n/a	n/a	MACP

Resilience: Low

Table 8 summarizes all populations that are classified as "low" for current resilience, rank order based on decreasing growth rate. Although these populations are small in size, many have very high growth rates in response to intensive management with recruitment clusters and translocation, which is critical for small populations. For example, 16 of the 33 populations within the low resilience category that could be classified have annual growth rates >5%, and an additional 8 populations are classified as increasing based on our criterion of $\lambda > 1.02$. However, 5 populations exhibit decreasing growth, and are less resilient, within this resilience category (Table 4).

Resilience: Very Low

Table 9 summarizes all populations that are classified as "very low" for current resilience, rank order based on decreasing growth rate. Many of these populations have been increasing, particularly critically small populations, in response to effective intensive management and with translocation to augment size and growth. Populations within this resilience category have a high risk of extirpation without intensive management. However, these small populations can be quite important for several reasons. With adequate potential habitat, these populations can grow and increase in resilience over time. Many of these smaller populations are near larger populations with which they are predicted to demographically merge and create larger, more resilient populations in the future. Finally, smaller populations increase species representation.

Many of the smaller populations are the only populations within some ecoregions (e.g. Cumberland Ridge Valley, Gulf Coast Prairie Marshes, and Mississippi River Alluvial Plain).

Table 8. Population resilience summary for “low” category sorted by descending lambda (λ). UA: data not available, n/a: not applicable due to missing data.

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Jones Ecological Research Center	32	Low	2015	2	1996	1.157	Increasing	EGCP
Silver Lake WMA	31	Low	2016	3	1998	1.139	Increasing	EGCP
Ocala National Forest A	58	Low	2016	7	1998	1.125	Increasing	FP
Ocala National Forest C	40	Low	2016	5	1998	1.122	Increasing	FP
Withlacoochee State Forest Croom	39	Low	2016	6	1998	1.110	Increasing	FP
Sabine National Forest A	32	Low	2016	19	2010	1.091	Increasing	UWGCP
Marine Corps Base Camp Lejeune A	33	Low	2016	7	1998	1.090	Increasing	MACP
Angelina National Forest C	51	Low	2016	32	2010	1.081	Increasing	WGCP
DeSoto District DeSoto National Forest B	53	Low	2017	25	2007	1.078	Increasing	EGCP
Manchester Poinsett	32	Low	2015	10	1998	1.071	Increasing	SH
Savannah River Site A	57	Low	2016	17	1998	1.070	Increasing	MACP
Goethe State Forest B	44	Low	2016	13	1998	1.070	Increasing	FP
Fort Jackson	41	Low	2016	13	1998	1.066	Increasing	SH
Savannah River Site B	35	Low	2016	12	1998	1.061	Increasing	SACP
Sam Houston National Forest F	35	Low	2016	20	2005	1.052	Increasing	UWGCP
Ouachita National Forest A	71	Low	2016	50	2009	1.051	Increasing	OM
Marine Corps Base Camp Lejeune B	91	Low	2016	41	1998	1.045	Increasing	MACP
Big Cypress National Preserve A	83	Low	2016	62	2009	1.043	Increasing	FP
Sam Houston National Forest B	67	Low	2016	47	2005	1.033	Increasing	UWGCP
Avon Park Air Force Range	35	Low	2016	21	2000	1.032	Increasing	FP
Withlacoochee State Forest Citrus	82	Low	2016	50	1998	1.028	Increasing	FP
Piedmont NWR-Oconee National Forest-Hitchiti Experimental Forest	83	Low	2016	53	1998	1.025	Increasing	P
Babcock Webb WMA	41	Low	2015	27	1998	1.025	Increasing	FP
Camp Blanding	31	Low	2016	24	2005	1.024	Increasing	SACP
Brosnan Forest	86	Low	2015	67	1998	1.015	Stable	SACP
Sandy Island	46	Low	2015	36	1998	1.015	Stable	MACP
Felsenthal-TNC	35	Low	2016	28	2000	1.014	Stable	UWGCP
Croatan National Forest	69	Low	2013	59	1999	1.011	Stable	MACP
Kisatchie District Kisatchie National Forest C-Peason Ridge	42	Low	2015	43	2003	0.998	Decreasing	WGCP
Holly Shelter Game Land	36	Low	2016	38	1999	0.997	Decreasing	MACP
Three Lakes WMA	45	Low	2016	50	2000	0.993	Decreasing	FP
Davy Crockett National Forest A	59	Low	2017	63	2012	0.987	Decreasing	UWGCP
Kisatchie District Kisatchie National Forest A	38	Low	2016	53	1998	0.982	Decreasing	WGCP
Georgia Safe Harbor	97	Low	2016	UA	UA	n/a	n/a	EGCP
Chickasawhay District DeSoto National Forest	69	Low	2016	47	2012	n/a	n/a	EGCP
Catahoula B Kisatchie National Forest	57	Low	2016	60	2014	n/a	n/a	WGCP
DeSoto District DeSoto National Forest A	47	Low	2017	47	2016	n/a	n/a	EGCP
Palmetto-Peartree Preserve Complex	43	Low	2015	UA	UA	n/a	n/a	MACP

Table 9. Population resilience summary for “very low” category sorted by descending lambda (λ). UA: data not available, n/a: not applicable due to missing data, and *: growth rates for the demographic population were computed and estimated in the absence of demographic population data according to abundance for all RCWs at the entire property level across multiple demographic populations.

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Sam Houston National Forest C	4	Very Low	2016	3	2005	1.333	Increasing	UWGCP
Talladega	14	Very Low	2015	3	2009	1.293	Increasing	CSRV
Ouachita National Forest B	5	Very Low	2016	1	2009	1.258	Increasing	OM
Dupuis Wildlife and Environmental Area	16	Very Low	2015	3	2007	1.233	Increasing	FP
Picayune Strand State Forest A	5	Very Low	2016	1	2008	1.223	Increasing	FP
Fort Gordon	24	Very Low	2015	2	1998	1.157	Increasing	SH
Shoal Creek District-Talladega National Forest	23	Very Low	2015	2	1998	1.155	Increasing	CSRV
Sabine National Forest C	7	Very Low	2016	3	2010	1.152	Increasing	WGCP
Winn District Kisatchie National Forest B	21	Very Low	2017	4	2002	1.117	Increasing	WGCP
TNC Disney Wilderness Preserve	9	Very Low	2016	4	2008	1.107	Increasing	FP
Okefenokee NWR A	11	Very Low	2015	2	1998	1.105	Increasing	SACP
Piney Grove	14	Very Low	2016	3	1999	1.095	Increasing	MACP
Picayune Strand State Forest B	13	Very Low	2016	3	1999	1.090	Increasing	FP
Ocala National Forest B	20	Very Low	2016	5	1998	1.080	Increasing	FP
Sabine National Forest B	22	Very Low	2016	14	2010	1.078	Increasing	WGCP
Warren Prairie Natural Area	13	Very Low	2016	4	2000	1.076	Increasing	UWGCP
Bull Creek Triple N WMA	18	Very Low	2016	7	2003	1.075	Increasing	FP
Sam Houston National Forest D	15	Very Low	2016	7	2005	1.072	Increasing	UWGCP
Military Ocean Terminal Supply Point	19	Very Low	2015	6	1998	1.070	Increasing	MACP
Pine City Natural Area	3	Very Low	2016	1	1998	1.063	Stable	MRAP
Lewis Ocean Bay Heritage Preserve	11	Very Low	2015	4	1998	1.061	Increasing	MACP
Okefenokee NWR C	9	Very Low	2015	6	2008	1.060	Increasing	SACP
Conecuh National Forest B	25	Very Low	2016	9	1998	1.058	Increasing	EGCP
Big Cypress National Preserve B	5	Very Low	2016	3	2007	1.058	Increasing	FP
Okefenokee NWR D	13	Very Low	2015	9	2008	1.054	Increasing	SACP
Davy Crockett National Forest B	25	Very Low	2017	12	2002	1.050	Increasing	WGCP
Angelina National Forest A	16	Very Low	2016	9	2004	1.049	Increasing	WGCP
Yawkey Wildlife Center	15	Very Low	2015	7	1998	1.046	Increasing	MACP
Catahoula A Kisatchie National Forest-Winn Kisatchie National Forest	12	Very Low	2016	7	2002	1.039	Increasing	WGCP
Babcock Ranch Preserve	12	Very Low	2017	10	2012	1.037	Increasing	FP
Okefenokee NWR B	15	Very Low	2015	12	2008	1.032	Increasing	SACP
Hal Scott-Stanton	20	Very Low	2016	13	1999	1.026	Increasing	FP
Corbett WMA	17	Very Low	2014	12	1998	1.022	Increasing	FP
St. Sebastian River Preserve State Park	13	Very Low	2016	9	1999	1.022	Increasing	FP
Bienville National Forest B	25	Very Low	2015	106*	1998*	1.020	Increasing	UEGCP
Webb Wildlife Center	14	Very Low	2015	10	1998	1.020	Stable	SACP
Bienville National Forest C	10	Very Low	2015	106*	1998*	1.020	Stable	UEGCP
Big Branch Marsh NWR	20	Very Low	2016	15	2000	1.018	Stable	GCPM
Platt Branch Wildlife and Environmental Area	6	Very Low	2016	5	2004	1.015	Stable	FP
McCurtain County Wilderness Area	14	Very Low	2015	11	1998	1.014	Stable	OM
Goethe State Forest A	22	Very Low	2016	17	1998	1.014	Stable	FP
Angelina National Forest B	6	Very Low	2016	6	2010	1.000	Stable	WGCP
Kisatchie District Kisatchie National Forest B	5	Very Low	2016	5	1998	1.000	Stable	WGCP
Sam Houston National Forest E	3	Very Low	2016	3	2005	1.000	Stable	UWGCP
Upper Ouachita NWR	1	Very Low	2016	1	1998	1.000	Stable	UWGCP
Sam D. Hamilton Noxubee NWR B	28	Very Low	2016	29	2007	0.996	Decreasing	UEGCP

Table 9. Continued.

Population	Current Pop Size	Current Baseline Category	End Pop Date	Initial Pop Size	Initial Pop Date	λ	Growth Category	Ecoregion
Catahoula C Kisatchie National Forest	6	Very Low	2016	7	1998	0.991	Decreasing	WGCP
Oakmulgee District B Talladega National Forest	5	Very Low	2016	6	2003	0.986	Decreasing	UEGCP
D'Arbonne NWR	3	Very Low	2016	4	1999	0.983	Decreasing	UWGCP
Persanti Island	2	Very Low	2016	3	1998	0.978	Decreasing	MACP
Holly Shelter Game Land B	1	Very Low	2016	2	1999	0.960	Decreasing	MACP
Holly Shelter Game Land C	1	Very Low	2016	2	2000	0.958	Decreasing	MACP
Sam D. Hamilton Noxubee NWR A	3	Very Low	2016	9	2007	0.885	Decreasing	UEGCP
North East North Carolina B	24	Very Low	2016	UA	UA	n/a	n/a	MACP
Corbett Private Land	22	Very Low		UA	UA	n/a	n/a	MACP
Crowell Lumber	21	Very Low	2015	21	2011	n/a	n/a	WGCP
Winn District Kisatchie National Forest A	21	Very Low	2017	20	2013	n/a	n/a	WGCP
Northeast North Carolina C	19	Very Low	2016	UA	UA	n/a	n/a	MACP
Mitchell Lake	10	Very Low	2017	UA	UA	n/a	n/a	P
Longleaf Heritage Preserve - Lynchburg Savanna Heritage Preserve WMA	8	Very Low	2015	6	2012	n/a	n/a	MACP
St. Marks NWR B	6	Very Low	2017	3	2016	n/a	n/a	EGCP
Jones State Forest	4	Very Low	2017	UA	UA	n/a	n/a	UWGCP
Northeast North Carolina D	4	Very Low	2016	UA	UA	n/a	n/a	MACP
Fairchild State Forest	2	Very Low	2017	UA	UA	n/a	n/a	UWGCP
Georgia Safe Harbor B	2	Very Low	2016	UA	UA	n/a	n/a	EGCP
Georgia Safe Harbor C	2	Very Low	2016	UA	UA	n/a	n/a	EGCP
Felsenthal NWR	1	Very Low	2016	UA	UA	n/a	n/a	UWGCP
Northeast North Carolina E	1	Very Low	2016	UA	UA	n/a	n/a	MACP
Northeast North Carolina F	1	Very Low	2016	UA	UA	n/a	n/a	MACP
Northeast North Carolina G	1	Very Low	2016	UA	UA	n/a	n/a	MACP
Northeast North Carolina H	1	Very Low	2016	UA	UA	n/a	n/a	MACP

Current Species Representation and Redundancy

Representation provides the ability of a species to adapt to changing environmental conditions. As described in Chapter 3, representation for this species is assessed primarily on life history variation and ecological diversity among ecoregions. This approach is based ecoregions that represented recovery units in the RCW Recovery plan (USFWS 2003).

Redundancy describes the ability of a species to withstand catastrophic events. Measured by the number of populations, their resiliency, and their distribution and connectivity, redundancy increases the probability that the species has a margin of safety to withstand or recover from catastrophic events (such as a rare destructive natural event or episode involving many populations). We report redundancy for RCWs as the total number and resilience of demographic populations and their distribution within and among representative units.

The historical range of the RCW included the entire historical range of longleaf pine ecosystems, but the RCWs also inhabited open shortleaf, slash, loblolly, and Virginia pine forests, especially in the Ozark-Ouachita Highlands and the southern tip of the Appalachian Highlands (Costa and Walker 1995). Occasional occurrences were noted for New Jersey (Hausman 1928), Pennsylvania (Gentry 1877), Maryland (Meanly 1943), and Ohio (Dawson and Jones 1903). Historic distribution data in Figure 25 consists of county level information based on published sources (Jackson 1971; Hooper et el. 1980; Costa and Walker 1995) and interviews with various RCW experts. County historical records are contemporary data, most from the 1900s, and do not represent pre-settlement conditions when RCWs were more abundant and probably more widely distributed.

Based on these data, RCWs no longer occur in 7 ecoregions where their occurrence in suitable woodland likely was on the edge the historic range: Ozarks, Central Mixed Grass Prairies, Interior Low Province, Cross Timbers and Southern Mixed Grass Prairies, North Atlantic Coast, Central Appalachian Forest, and Southern Blue Ridge (Figure 24). RCWs have been extirpated from these ecoregions for some time, and they are not considered relevant to recovery (USFWS 2003). The remaining 13 ecoregions still contain RCWs.

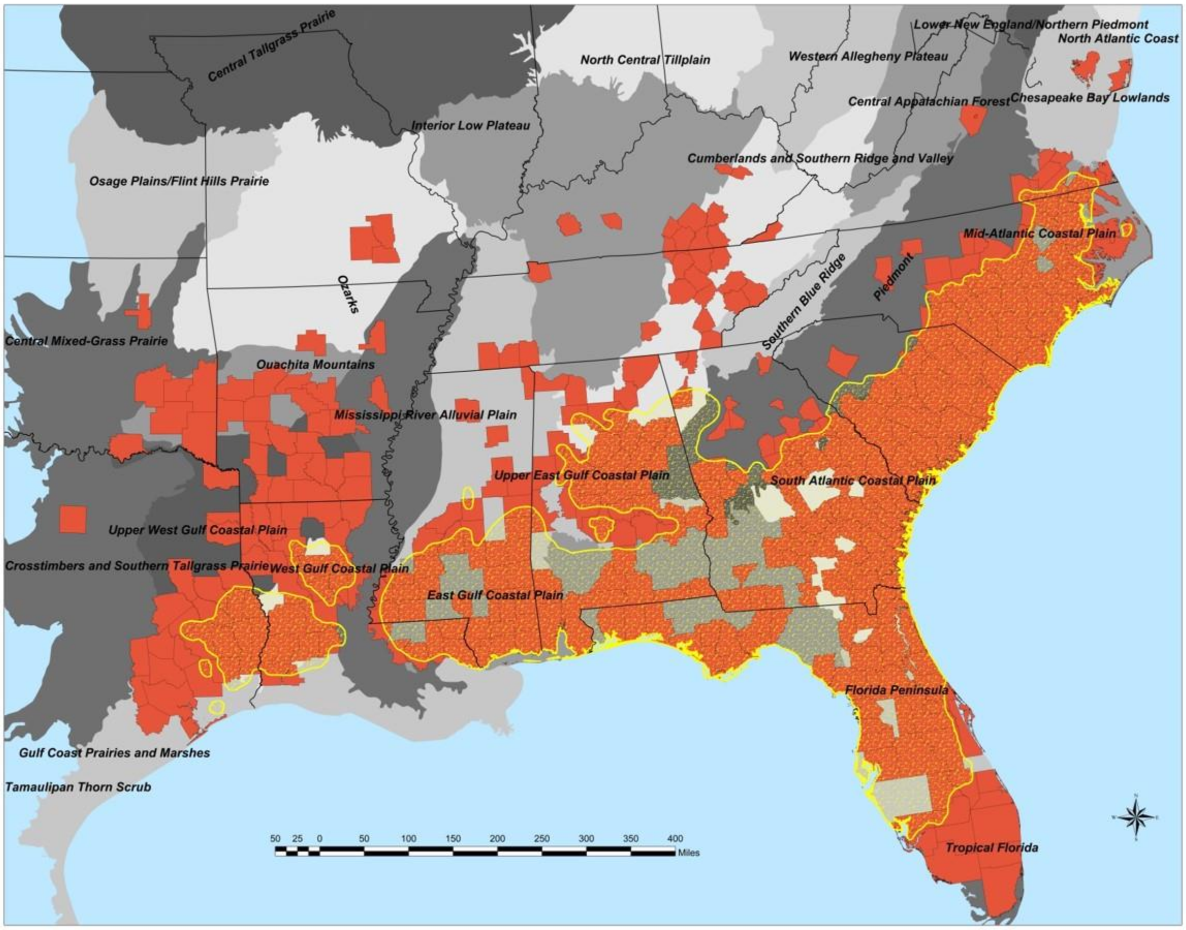


Figure 25. Historic RCW county distribution, from Costa and Walker 1995, with ecoregions. Historical distribution of longleaf pine in yellow stipple.

Table 10 summarizes current redundancy and representation by resilience categories according to population size and distribution within and among representative units (i.e., physiographic regions). Although the Mid-Atlantic Coastal Plain contains the most RCW populations (24), it only has 1 highly resilient population and 1 moderately resilient population; the remaining populations are of low or very low resilience categories. The Mississippi River Alluvial Plain only has one population, which is very low in resilience. Of the 13 ecoregions with current populations, those with high (3) and very high resilience (3) are restricted to only 4 regions: Mid-Atlantic Coastal Plain, East Gulf Coastal Plain, South Atlantic Coastal Plain, and Sandhills. Only 2 ecoregions, the East Gulf Coastal Plain and the Sandhills, have more than 1 population classified as of high or very high resilience, and only these 2 regions have more than 2 populations classified as moderately to very high resilience. Redundancy in the Sandhills is notable because of 6 different populations, 2 are in the high and very high resilience category.

Table 10. Redundancy and representation summary for RCW. Ecoregions: CAF (Central Appalachian Forest (CAF), CMGP (Central Mixed Grass Prairie); CSRV (Cumberland Ridge Valley); CT (Cross Timbers); EGCP (East Gulf Coastal Plains); FP (Florida Peninsula); GCPM (Gulf Coast Prairie Marshes); ILP (Interior Low Plateau); MACP (Mid-Atlantic Coastal Plains); NAC (North Atlantic Coast); OM (Ouachita Mountains); OZ (Ozark Mountains); P (Piedmont); SACP (South Atlantic Coastal Plains); SBR (Southern Blue Ridge); SH (Sandhills); UWGCP (Upper East Gulf Coastal Plains); UWGCP (Upper West Gulf Coastal Plains); WGCP (West Gulf Coastal Plains); MRAP (Mississippi River Alluvial Plain).

Past-to-Current Redundancy and Representation						
	Resilience Size-Class Category					
Ecoregion	Very Low	Low	Moderate	High	Very High	Total
MACP	16	6	1	1	0	24
FP	13	9	0	0	0	22
WGCP	11	4	2	0	0	17
UWGCP	9	5	1	0	0	15
EGCP	4	6	2	0	2	14
SACP	5	3	1	1	0	10
UEGP	5	0	2	0	0	7
SH	1	2	1	1	1	6
OM	2	1	0	0	0	3
CRV	2	0	0	0	0	2
P	1	1	0	0	0	2
GCPM	1	0	0	0	0	1
MRAP	1	0	0	0	0	1
OZ						
CMGP						
CT						
SBR						
NAC						
CAF						
Total	71	37	10	3	3	124

Only 4 ecoregions (South Atlantic Coastal Plain, Mid-Atlantic Coastal Plain, West Gulf Coastal Plain, Upper East Gulf Coastal Plain) have 2 populations of moderate to high resilience, and thus some level of redundancy in terms of relatively resilient populations. Most of the redundancy in these 4 regions is by populations that are only moderately resilient. There is 1 ecoregion (Upper West Gulf Coastal Plain) with a single moderately resilient population. All of the populations in the remaining six ecoregions are of low or very low resilience, but are important for representation in their respective regions and across the range. Five (Ouachita Mountains, Cumberland Ridge and Valley, Piedmont, Gulf Coast Prairie Marshes, and Mississippi River Alluvial Plain) of these 6 ecoregions contain 3 or fewer populations. For example, populations in the Ouachita Mountains represent the northwestern range limit in shortleaf pine-bluestem communities. Populations in the Cumberland Ridge and Valley include interior mountain longleaf pine habitat. The single critically small population in the Mississippi River Alluvial Plain occurs in native loblolly pine on a high terrace. And in the Florida Peninsula, southern regions represent the extreme southern range of the species in south Florida slash pine that is restricted to the southern peninsula.

In summary, representation for RCW has decreased significantly relative to the historical distribution of the species. Not only have RCWs historically inhabited several ecoregions where they no longer occur, they were also once much more abundant within ecoregions they now occupy. In fact, in many ecoregions the species likely was continuously distributed over vast areas historically, rather than distributed in isolated patches as RCWs are today (Conner et al. 2001a). However, representation in terms of the species presence and absence has not decreased further since 2003 when the current Recovery Plan was developed and subsequently implemented (USFWS 2003). Currently, redundancy of moderately to very highly resilient populations is low within ecoregions (Table 10). The total number of populations gives the appearance of greater redundancy, as 6 of the 13 ecoregions have 10 or more populations, and 8 of 13 ecoregions contain 6 or more populations, but this redundancy is manifested in populations of low or very low resilience. Over the entire range, there are 6 populations with high or very high resiliency, and 16 with moderate to very high resiliency (Table 10).

CHAPTER 5: INFLUENCES ON VIABILITY

For the RCW to maintain viability, its populations or some portion thereof must be resilient. Stochastic events that have the potential to affect RCW populations include wildfires, drought, and intense storm events such as hurricanes, tornadoes, and ice storms. A number of other risk factors influence the resiliency of populations, including southern pine beetle outbreaks, sea level rise, land use changes, invasive species, kleptoparasitism, and management dependence (e.g., artificial cavities and prescribed fire). Influencing those factors are elements of RCW ecology and habitat (see factors) that determine whether RCW populations can grow to maximize habitat occupancy, thereby increasing the resiliency of populations. These influences on viability are discussed below.

Hurricanes and Other Storm Events

Hurricanes are naturally occurring frequent disturbances that, with frequent fire, historically shaped forest community composition and structure, particularly in the presettlement longleaf pine ecosystem occupied by RCWs (Mitchell and Duncan 2009), but also represent the greatest potential catastrophic threat to RCW population viability. Managing the beneficial and undesirable consequences of these disturbance regimes in our modified contemporary environment is vital to sustain viable populations. Hurricanes, tornadoes, severe thunderstorms, and ice storms damage, blow down, snap, and otherwise kill pines used for cavities and foraging. From 2003 to 2011, the centerline of 16 hurricanes, including 7 major hurricanes, and 14 tropical storms at landfall subsequently tracked within 30 miles of 56 properties representing 38 of the 39 designated recovery populations in the 2003 recovery plan (McDearman 2013, unpublished). Single hurricanes during this period frequently tracked within this distance affecting more than 1 of these populations, and populations in the Florida peninsula experienced more frequent hurricanes or tropical storms than elsewhere. Impacts of these hurricanes and tropical depressions varied, but none were as devastating as Hurricane Hugo in 1989.

The devastation wrought by Hurricane Hugo on the population inhabiting the Francis Marion National Forest demonstrated all too clearly that such storms can produce catastrophic changes (Hooper et al. 1990). Hurricane Hugo, a major category 4 hurricane at landfall, significantly reduced the large Francis Marion National Forest RCW population from about 480 to 384 active territories with the loss of 87 percent of all cavity trees and mortality to 63 percent of all RCWs (Watson et al. 1995). In response to intensive management immediately after the hurricane with extensive installation of artificial cavities (Watson et al. 1995) and continued artificial cavity and habitat management afterwards, the Francis Marion population today consists of 469 active RCW territories. Thus, large coastal populations are capable of avoiding extirpation by catastrophic hurricanes, but post-storm recovery requires continuous and intensive management for decades for populations to recover to pre-storm conditions.

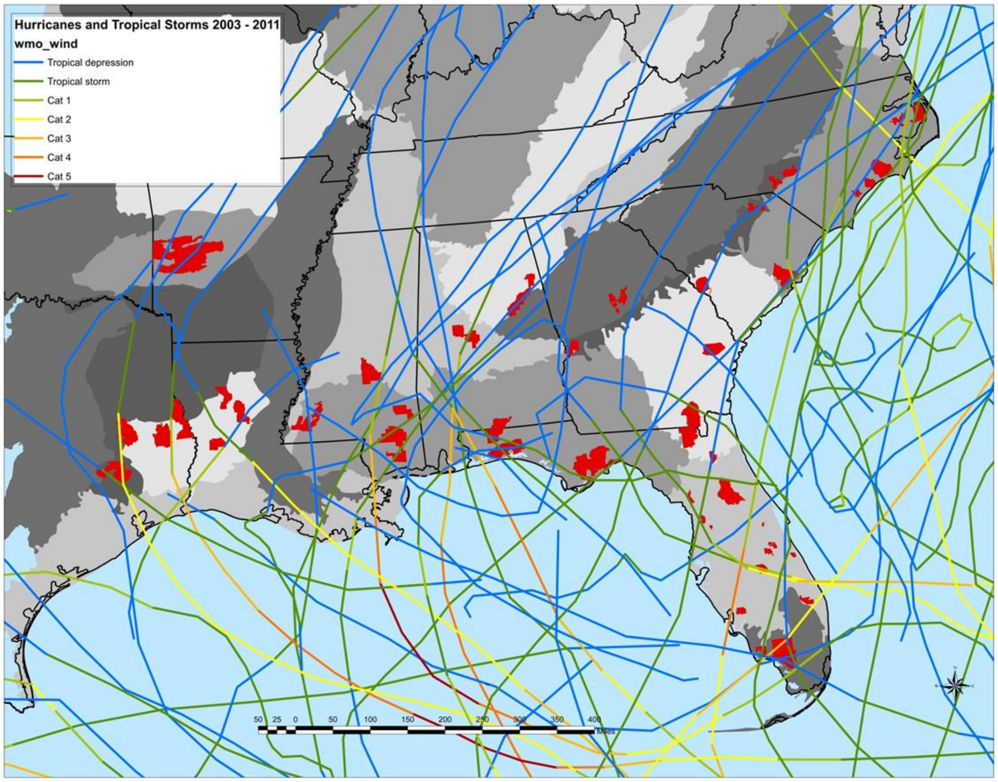


Figure 26. Tropical storm and hurricane centerline tracks, 2003 – 2011, relative to properties for 39 populations designated for recovery in the 2003 recovery plan.

Research and management experiences in response to Hugo remain applicable to storm management responses today, including an increased awareness of the risk that hurricanes can extirpate small populations and severely impact large populations. Individual and recurring hurricanes can reduce or virtually deplete available RCW cavities and foraging habitat with direct and indirect losses to the number of RCW potential breeding groups depending on storm intensity, width, proximity and other factors. Heavy and prolonged rainfall during tropical depressions and storms that do not destroy cavities or foraging habitat can cause RCW nestling, fledgling, and adult mortality (Conner et al. 2005, Keys unpublished). Hazardous fire fuel loads from blow-down of small and large woody debris, with dead or dying standing trees, can impair or eliminate the continued use of prescribed fire to restore and maintain habitat. Effects of Hurricane Hugo are probably the most well-known and studied case history, although other sources are available as well (Jones 1989, Hooper et al. 1990, Engstrom and Evans 1990, Hamrick 1992, Loope et al. 1994, Hooper and McAdie 1995, Lipscomb and Williams 1995, Loeb and Hooper 1997, Williams and Lipscomb 2002, Hooper et al 2004, Lohr et al. 2004, Hoyle 2008, Lopez 2008, Bainbridge et al. 2011).

Table 11**.** Regional hurricane return periods in years (from Parisi and Lund 2008).

Saffir-Simpson Category	FL	Gulf States (TX, LA, MS, AL)	East Coast (GA to ME)
1	1.7	1.6	1.6
2	2.4	2.1	2.4
3	3.3	2.8	4.2
4	6.5	5.6	28.7
5	23.4	37.1	NA

Because of the distribution of RCWs, most coastal or lower coastal plain populations face a significant risk from major hurricanes, although there is little risk of significant impacts to large inland populations by hurricanes of any magnitude (Hooper and McAdie 1995). Using the HURISK model (Neumann 1987), Hooper and McAdie (1995) estimated average hurricane return intervals for 13 selected RCW population properties. Overall, hurricane return intervals for near coastal populations (e.g. within 50 miles of the coast) evaluated (e.g., Francis Marion National Forest, Croatan National Forest, Apalachicola National Forest, Eglin Air Force Base-Blackwater River State Forest-Conecuh National Forest, and DeSoto National Forest) were about 14-21 years for Category 1, 43-55 years for Category 2, 90-130 years for Category 3, and 260-400 years for Category 4 hurricanes. Inland sites (e.g., Bienville National Forest, Piedmont NWR-Oconee National Forest, Oakmulgee Ranger District-Talladega National Forest, and Talladega District-Talladega National Forest) 140 or more miles from the coast had Category 1 return intervals of 170 to more than 500 years, and more than 500 years for all greater storm categories. Interpreting these and related results from the 1995 analysis to all current and future RCW populations requires caution because the intensity and frequency of hurricanes has increased since the early 1980s and are predicted to increase further in response to future climate warming (Melillo et al. 2014). Moreover, other more recent methods to estimate hurricane return and strike probabilities (e.g. Trepanier and Scheitlin 2014, Ellis et al. 2014) are available, but have not been applied specifically to RCW populations. For general perspective (Table 11), average return probabilities of storms with hurricane force winds intercepting Gulf and eastern coastlines estimated by other recent methods ranged from 1.6 years for category 1 storms to 37.1 years for category 5 storms in Gulf states (Parisi and Lund 2008).

On October 10, 2018 near Mexico Beach, FL, Hurricane Michael made landfall as a category 4 storm affecting three demographic populations: Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest, Silver Lake WMA, and Jones Ecological Research Center. Past, and future, models for these simulations were completed prior to this hurricane. Although the storm centerline passed west of Apalachicola National Forest, hurricane force winds damaged or blew down 1,409 cavity trees. National Forest personnel assessed 870 clusters and installed 717 artificial cavities to provide at least four suitable cavities for each cluster. According to National Forest Service personnel, only a small number of active clusters were expected to be lost. At

Tate's Hell State Forest, 23 of 527 cavity trees were blown down; only six clusters required and were provisioned with artificial cavities. Storm damage was minor at St. Marks National Wildlife Refuge (NWR), which is located further east, and only a few artificial cavities were required. Elsewhere, the hurricane damaged and destroyed cavity trees in the smaller Silver Lake Wildlife Management Area and Jones Ecological Research Center populations. At Silver Lake WMA, at least 103 of 207 cavity trees were lost, and artificial cavities were installed to reduce the risk of active clusters loss. Artificial cavities were provisioned to minimize the impact of the loss of about 25% of all cavity trees at the Jones Ecological Research Center. In September, 2018 Hurricane Florence struck the North Carolina coast, destroying 157 cavities on Marine Corps Base Camp Lejeune. Forty-one artificial cavities were installed, ensuring that all 119 clusters housing breeding groups retained a sufficient number of cavities. More accurate post-storm population size data will be available for all of these affected populations following completion of 2019 breeding season surveys.

Natural hurricane-fire interactions in a pre-settlement landscape probably involved more intense post-storm fire in response to additional fuel loads from trees, branches, and foliage blown to the ground (Myers and Van Lear 1998, Liu et al. 2008). Today, hazardous fire fuel loads from blow-down of small and large woody debris, with dead or dying standing trees, will impair or eliminate the continued use of prescribed fire to restore and maintain open pine habitat without effective management (Myers et al. 1998, Bryant and Boykin 2007, Guan 2014). Post-hurricane management since 2003 on federal and state lands typically has involved surveys followed by installation of artificial cavities to reduce effects of cavity loss, and in most cases additional management to reduce hazardous fire fuels to sustain an effective prescribed fire program to maintain or restore habitat (McDearman, unpublished). Post-storm management is critical to reduce adverse effects. For example, 107 of the 156 cavity trees on the DeSoto Ranger District, DeSoto National Forest, were destroyed by Hurricane Katrina, but 90 artificial cavities were installed within 3 weeks of the storm. Because many animals other than RCW use RCW cavities, competition from other animals for cavities for roosting and nesting could increase as a result of the shortage of available cavities caused by hurricane damage (Engstrom and Evans 1990). Hurricanes will inevitably and regularly strike woodpecker populations. Any strategy to ensure species and population viability must address this form of catastrophe.

Catastrophic high-intensity hurricanes are not the only storm type impacting RCWs and their habitat. Other storms impacting RCWs include tornadoes, tropical storms, ice storms, downbursts, and prolonged rain events, amongst others. Regardless of the storm type, RCWs and their habitat are impacted in several general ways.

Foraging Habitat Loss

Snapped and down pines from a storm represent suitable or potentially suitable foraging habitat loss in RCW territories. Apart from the maximum sustained wind and wind gusts, other factors potentially affecting loss of pines include species, soil type, stand/forest density, and the availability of suitable habitat. Evidence indicates that longleaf pine is more resistant to breakage and blow down than other pines. Pines on wet or highly organic soils are more susceptible to tip over. Open, sparsely stocked stands or stands bordering open areas are more likely to experience loss with greater incursion from wind, turbulence, and wind gusts.

Direct post-storm management effectiveness and opportunities to enhance impaired habitat are limited. The loss of suitable and potentially suitable pines for foraging cannot be immediately mitigated by management, which depends on additional growth and recruitment of pines in limited territories over a long period of time. Most immediate forest management actions are intended to secure remaining habitat by salvage and removal of snapped, severely damaged and stressed standing trees that are a risk for future pine or other beetle outbreaks that may kill and reduce remaining habitat.

Cavity Loss

Cavities are lost either by blow down or snapped trees (Bainbridge et al. 2011). Evidence indicates that snapped trees with artificial cavity inserts tend to break at the insert, relative to natural and drilled cavities. Cavity tree loss data from published papers are available from Hurricanes Hugo and Rita, but other data when available are largely unreported. The cavity type and category of a storm or the estimated maximum sustained wind speed at a population are not the only factors affecting cavity tree loss. As described for foraging habitat, other factors include soil type and stand density.

Post-storm cavity management involves assessments of the number and suitability of cavities in affected territories, with installation of artificial cavity inserts or drilled cavities to provide at least 4 suitable cavities per cluster. Cavity management is critical to sustain active territories and potential breeding groups in suitable, but cavity limited, habitat. The past history of storm management responses indicate that federal and state agencies are likely to implement cavity management. Resources and management objectives of most private landowners are unlikely to result in intensive post-storm cavity management.

Habitat Degradation

As used here, habitat degradation is different from the direct loss of cavities and pines for foraging habitat. Intense storms generate large and small woody debris on the forest floor and create canopy gaps at different scales to increase sunlight. Depending on the extent of disturbance, woody debris represents hazardous fire fuels. Additional sunlight to the understory and forest floor will stimulate growth of shrubs and hardwoods, particularly at sites with marginal and poor RCW habitat quality where small surviving hardwoods will be released for accelerated growth to the midstory or canopy. Prescribed fire programs that have been effective at controlling adverse hardwood midstory encroachment may be either impossible or delayed until other mitigating fuel treatments can be applied. In these conditions, a loss or reduction of prescribed fire programs over time following a storm may lead to further habitat degradation.

Tropical depressions and tropical storms are unlikely to create serious or widespread hazardous fuels and forest gaps to release temporarily suppressed hardwoods across large areas, but can be important for post-storm management in small populations. Quantifying or characterizing these parameters for hurricanes will require careful consideration.

Mortality

Storms directly cause RCW mortality by impaling or crushing birds in cavities in trees that snap at cavities or in cavity trees blown to the ground. Presumably, at least some RCWs are killed in flight by strong winds or hail, although there is no substantial data to this effect. Tropical storms and depressions are not expected to cause significant cavity tree loss or damage, but long torrential rains associated with these storms and hurricanes, depending on the time of year, can cause mortality by adversely affecting feeding rates of nestlings as well as foraging by adults (Conner et al. 2005 and unpublished data). Mortality affects group size and composition in post-storm territories that remain suitable with sufficient cavities, and potentially to such an extent that a suitable territory is unoccupied.

Southern Pine Beetles

The southern pine beetle is a species of bark beetle native to the forests of southern United States, Mexico, and Central America. It is considered one of the most important causes of economic loss in forestry with about $900 million worth of damage caused from 1960-1990 in the southern United States (Meeker et al. 2000). The adult beetle excavates an entrance through the bark and then creates S-shaped tunnels in the cambium tissue, just beneath the bark. This disrupts the flow of nutrients, killing the tree in typically 2-4 months. Most trees resist the initial attacks by secreting resin that can "pitch out" some adults and slow the entry of others, but trees almost always die as their defenses are overwhelmed by thousands of attacking beetles.

The impact of southern pine beetles on RCWs is on the cavity trees, not the birds—at least not directly. Outbreaks of sufficient size to constitute a catastrophe at the population level will likely be restricted to smaller populations dependent on tree species other than longleaf pine. Southern pine beetle infestation is not normally a problem in longleaf pines because of this species' copious production of pine resin that serves as a defense against beetle infestation (Hodges et al. 1977, Conner and Rudolph 1995b). Loblolly and shortleaf pines produce less resin and thus are generally more susceptible to infestation. Southern pine beetles are the major cause of cavity tree death on Texas national forests (Conner et al. 1991a) where, for example, more than 350 cavity trees were killed by southern pine beetles during a major infestation on the Sam Houston National Forest between 1983-1985 (Conner et al. 1991a).

Wildfire

Fire is an integral component of the southern pine/bunchgrass ecosystems of the southeastern United States, and fire suppression is a principal factor in the decline of these ecosystems and characteristic species such as the RCW. Prior to European colonization, there were few natural firebreaks in the southeast, so fires burned for extended periods over large areas. Return intervals for these natural fires were as frequent as 1 to 3 years in much of the Atlantic and Gulf Coastal Plain, and as frequent as 4 to 6 years in Upper Gulf Coastal Plain and the Piedmont (Wahlenburg 1946, Frost 1998). Some areas, such as slopes with northern aspect and wetlands, may have burned at frequencies of 7 to 25 years (Frost 1998).

Fire intensity is intimately related to fire frequency, and together they are a primary determinant of ecosystem structure and species composition. Over much of the southeast, frequent fires were low in intensity, as evidenced by the species adaptations and structure of longleaf and shortleaf communities (below). In some regions, fires were less frequent and of stand-replacing intensity. Through historic fire suppression, frequency of fire was substituted for intensity, (i.e., frequent, low-intensity fires versus infrequent, catastrophic wildfires), and a fire-deprived longleaf forest now responds differently to fire than it did historically, when fire was much more frequent.

A potential fire risk in fire suppressed longleaf pine stands is the accumulated mounds of pine straw and humus (also called duff) around the base of trees. The duff often is several inches deep and, if dry, fire will smolder for hours or days and will ultimately result kill affected trees.

The accumulation of hazardous large and small fuels in RCW habitat can be a significant impediment to a continuing program of prescribed fire to maintain and restore habitat. When treated, hazardous fuels usually are reduced by commercial and non-commercial salvage of down or severely damaged timber and mulching of other debris and small diameter excessive hardwoods. Timber salvage operations on federal lands today is primarily to achieve ecological restoration, although a prompt response for a commercial salvage sale is important to achieve ecological objectives while supporting local economies. Salvage operations by state and private landowners may more commonly focus on economic objectives, although these also can be ecologically critical. The costs of mulching for restoration tend to restrict these operations to federal agencies.

Kleptoparasitism and Other Heterospecific Interactions

If a cavity created and used by RCWs is usurped by another species, the interaction between species is termed cavity kleptoparasitism (Kappes 1997). Cavity kleptoparasitism may negatively affect individual woodpeckers or woodpecker groups on occasion (see below). Occasional loss of nests or cavities is unlikely to have population-level impacts in RCW populations that are healthy and of medium to large size. However, critically small populations or isolated groups may not be able to tolerate high rates of kleptoparasitism. Also, effects of kleptoparasites may vary with habitat quality. Two common kleptoparasites are red-bellied woodpeckers and southern flying squirrels.

Usurpation of cavities by red-bellied woodpeckers and other species may result in open roosting for RCWs. For example, Kappes (1997) observed 15 adults open roosting during a winter in

Florida; 14 of these 15 had suffered loss of cavities to red-bellied woodpeckers. However, how much open roosting may affect survival or territory occupancy is not yet known. Rates of kleptoparasitism by red-bellied woodpeckers on RCWs may vary inversely with habitat quality (F. James, pers. comm.). Similarly, RCWs in optimal habitat are likely to suffer less impact from each usurpation event.

Reported rates of occupancy of RCW cavities by southern flying squirrels range from 9 to 34 percent (Dennis 1971, Rudolph et al. 1990a, Conner et al. 1997b, Loeb 1993, Laves and Loeb 1999, Mitchell et al. 1999). Southern flying squirrels prefer active cavities with non-enlarged entrance tunnels over those with entrance tunnels enlarged (Rudolph et al. 1990a, Loeb 1993), and cavity inserts over natural cavities (Lotter 1997). Among active cavities, southern flying squirrels prefer cavities with enlarged chambers over those with unmodified chambers (Rossell and Gorsira 1996).

Southern flying squirrels could potentially affect RCWs through usurpation of cavities or through predation. There is some disagreement among researchers over direct and indirect effects of cavity usurpation. Some suggest that cavity usurpation lowers nest attempts (Loeb and Hooper 1997), but others have found no evidence that the presence or abundance of southern flying squirrels increases open roosting or decreases nest attempts (Rudolph et al. 1990a, Conner et al. 1996, Laves 1996, Mitchell et al. 1999). Whether or not flying squirrels are significant predators of RCW nests is discussed below.

It has been suggested in the past that southern flying squirrels increase with increasing hardwood midstory (Conner and Rudolph 1989, Loeb et al. 1992). Yet, Conner et al. (1996) observed regular use of RCW cavities by southern flying squirrels in loblolly-shortleaf pine habitat with and without hardwood midstory and in open longleaf pine habitat that was nearly devoid of hardwood vegetation. Southern flying squirrels are abundant and ubiquitous, and at the present time the influence of plant species composition and vegetative structure on flying squirrel distributions is not understood.

Cavity enlargement by heterospecifics can be an issue for RCW. Enlarged cavities are those whose entrance tunnels have been widened by several species of woodpeckers (Conner et al. 1991a, Neal et al. 1992). Cavity enlargement is generally done by pileated woodpeckers, but red-bellied and red-headed woodpeckers and northern flickers also enlarge cavities created by RCWs (J. H. Carter III, pers. comm.). Pileated woodpeckers greatly expand or obliterate entrance tunnels and can also enlarge the cavity chamber if sufficient heartwood is present (Conner *et al.* 1991a). Over a period of 13 years in the Angelina National Forest in eastern Texas, pileated woodpeckers enlarged 41 percent (114 of 276) of unprotected natural RCW cavities (Saenz et al. 1998). Cavity enlargement by pileated woodpeckers can have strong negative impacts on individual RCWs and, more importantly, on the entire population.

The main predator for RCW are rat snakes, although flying squirrels have also been implicated. Rat snakes are excellent tree climbers (Jackson 1976) and frequently prey on cavity-nesting birds (Fitch 1963, Jackson 1970, Rudolph et al. 1990b). They attempt to climb cavity trees and trees with nests more often than expected by chance (Neal et al. 1993b). Sometimes, rat snakes are able to breach the resin barrier and prey on cavity contents such as eggs, nestlings, or even adults (Jackson 1978a, Neal et al. 1993b, 1998).

However, reports of individual predation events by rat snakes on RCWs are relatively scarce, and there is no evidence that such predation affects woodpeckers at the population level. For example, there was no difference in average reproduction between nests in cavity trees fitted with snake exclusion devices and untreated cavity trees over three years in the longleaf pines of northwest Florida (L. Phillips, unpublished). It is likely that the resin barrier is a highly effective means of deterring rat snakes, especially in longleaf pine (Rudolph et al. 1990b).

Although flying squirrels are known to eat RCW eggs on occasion (Harlow and Doyle 1990), there is little consistent evidence that flying squirrels significantly depress reproduction. Two experimental studies have been conducted comparing reproductive success of RCWs in clusters with and without squirrel removal (Laves and Loeb 1999, Mitchell et al. 1999). Laves and Loeb (1999) reported lowered reproduction in clusters without squirrel removal, resulting from increased whole brood loss in one year and increased partial brood loss in the following year. Mitchell et al. (1999) reported no difference in overall reproduction between clusters with and without squirrel removal, but noted increased partial brood loss in clusters that had squirrels removed. In addition, Conner et al. (1996) did not detect any relationship between abundance of southern flying squirrels and reproductive success of RCWs in eastern Texas. No study has yet shown an effect of flying squirrels on RCWs at the population level (Mitchell et al. 1999). Thus, it appears that impacts of flying squirrels on RCWs are not strong, at least in the populations in which they have been assessed. The dynamics of RCW predation in cavities by rat snakes and cavity usurpation by other species can be complex. Rat snake predation on RCW cavity kleptoparasites and predation by southern flying squirrels on red-bellied woodpeckers may indirectly provide a net benefit to RCWs and the availability of suitable cavities for their use (Kappes and Davis 2008, Kappes and Sieving 2011).

Land use/construction

The Endangered Species Act prohibits activities that could result in take of listed species. For example, land use and construction activities that adversely and incidentally affect RCWs by the destruction or alteration of habitat (e.g. harm) or that cause harassment would be subject to regulatory review and authorization by provisions of the Endangered Species Act under section 7(a)(2) for federal actions or section 10(a)(2)(A) for non-federal actions.

Formal section 7 consultations between federal agencies and the Service on adverse proposed land use actions in recent years have been limited primarily to effects of military training on

Department of Defense installations, with less frequent consultation with the U.S. Army Corps of Engineers for adverse direct and indirect effects by real estate development. All Army, Air Force and Marine Corps installations have RCW management plans and guidelines to limit adverse effects of military training. Otherwise, activities with incidental take of RCWs typically have included clearing forests for construction of training ranges and infrastructure. Affected populations, however, have remained stable or increased as a result of conservation management programs designed to maintain and restore habitat and continue to increase population size with recruitment clusters. Active and beneficial RCW management to increase population sizes on military installations has been an essential component of recovery and to offset adverse effects of training. Future potential impacts cannot be precisely predicted. If trends and impacts during the past decade with affirmative RCW conservation management are indicative of the future, adverse future impacts are not expected to cause a significant reduction to populations on military installations or the ability of installation managers to attain RCW recovery and related population size objectives.

Of all Department of Defense installations, Fort Benning probably has the greatest challenge to successfully integrate increased training with RCW conservation and recovery. Following Base Realignment and Closures and moving the Armor School from Fort Knox to Fort Benning, substantial construction was initiated with a significant increase in the frequency and types of training occurring on Fort Benning. The formal section 7 consultation for the proposed Maneuver Center of Excellence resulted in a jeopardy biological opinion issued by the Service with reasonable and prudent alternatives that included the acquisition of off-base properties to support maneuver training. The jeopardy opinion was subsequently withdrawn by the Service in response to a change in proposed training that reduced adverse impacts.

Today, all large Department of Defense installations are engaged in acquiring and protecting surrounding properties, whether by fee simple title or easements from willing sellers, to reduce adverse land uses and encroachment on private lands that would limit military training. For example, to further support potential future additional training demands, Marine Corps Base Camp Lejeune has developed the RCW Recovery and Sustainment Program (RASP) with the Service to identify, secure, and manage suitable off-base parcels to expand and increase the RCW population. Fort Benning is engaged in developing a similar program.

Forest management by the U.S. Forest Service, Department of Defense, Service, and other federal agencies by silvicultural operations to maintain and restore RCW habitat remains vital to sustain populations on these federal lands. These activities include thinning overstocked pine stands to create suitable foraging habitat, regeneration to sustain a future source of suitable habitat, and conversion of off-site pine stands to longleaf. As RCW population sizes and density have increased, the ability to convert offsite loblolly or slash pines to more sustainable and fire resistant longleaf is becoming a challenge at some sites. The availability of additional or excess habitat in RCW foraging partitions is limited at some sites to sustain a minimal amount and quality of habitat to avoid adverse effects when harvesting offsite pines in suitable habitat for conversion to longleaf. In other areas with natural loblolly or slash pines, old stands providing suitable RCW habitat need regeneration to sustain future habitat before naturally declining by senescence to unsuitable conditions. The Service anticipates a future need, via section 7 consultations, to authorize take incidental for silvicultural operations providing a long-term net beneficial effect with short-term adverse effects. The amount and extent of future short-term adverse effects cannot be precisely predicted. The RCW population at Fort Benning, probably more so than any other population on federal lands, currently exists with limited habitat on offsite and declining loblolly stands. Future take of RCWs incidental to beneficial long-term management may be greater at Fort Benning than elsewhere.

Land use and real estate development by non-federal entities that may take RCWs require either a habitat conservation plan and incidental take permit under section 10(a)(1)(B) of the ESA to mitigate adverse impacts, or authorization for such actions when permitted or licensed by a federal agency by formal section 7 consultation. Non-federal and private landowners enrolled in the RCW safe harbor program may incidentally take above-baseline RCWs, as authorized by the Service, that increased in response to landowner’s voluntary and beneficial management.

Conservation Management

Current RCW populations are highly dependent on active conservation management with prescribed fire, beneficial and compatible silvicultural methods to regulate forest composition and structure, the provision of artificial cavities where natural cavities are insufficient, translocation to sustain and increase small vulnerable populations, and effective monitoring to identify limiting biological and habitat factors for management. Apart from a future condition when forests consist of pines of suitable age, number and abundance for natural cavities, there is no future point or condition when RCW populations will not be dependent on continued active management due to the need to regularly apply prescribed fire. The vast majority of all current populations continue to depend upon artificial cavities. All of these future active management measures require substantial organizational resources with staff and funding at populations managed for conservation and recovery. Fiscal year budgets for federal, state, and other public agencies are not expected to increase in future years. Moreover, there is increasing uncertainty among some agencies on their ability to sustain future RCW conservation and management with other agency missions and objectives for their lands.

CHAPTER 6: FUTURE CONDITIONS

We assessed future condition for RCW populations by modeling past trends in population growth and size as a function of environmental and management covariates. We used the resulting models to project RCW populations 25 years into the future under different management scenarios. All analyses, unless otherwise noted, were performed in R (R Core Team 2017).

Past Population Growth Model

We assessed future RCW population growth, population size (active clusters) and resilience by first modeling past trends in demographically delineated populations as affected by environmental and management covariates with best fit (AIC) linear mixed effect models. Best fit models were developed from 87 demographically delineated populations with 914 observations of annual data. Annual data for past population delineations, size, habitat and management conditions were compiled from annual RCW property data reports and other information submitted to the Service. Additional population, habitat and management data were acquired from elicitations sent to property managers and biologists. The impact of hurricanes and other storms during 1998-2017 are included as a component of annual variation in population size. Missing data for certain populations for some years were estimated by imputation with an expectation-maximization algorithm following a pilot study on imputation methods and effects (Appendix 1). We distilled the collected data into the variables contained in Table 12. Time-series growth data were modeled as independent observations because there was no widespread evidence of temporal autocorrelation of growth rates.

All demographic populations with sufficient data were pooled by size class (small, medium, and large). Populations were separately modeled as small (6 – 29), medium (30-75), and large (>75) classes to fulfill linear model assumptions for distribution of residual errors. Populations with fewer than six active clusters were not modeled because of high variation in growth rates. While many models of population growth may be performed on individual populations, all RCW populations were combined by size-class to 1) increase the sample size and statistical power to estimate multiple covariate effects, with the assumption that populations respond similarly to covariates, and 2) to estimate both within- and between- population parameters. For example, management inputs could vary over time within a population, while dominant pine as we defined it only varied across populations. Combining all populations in the past model also allowed us to create a global model of RCW population growth not tied to a specific population, enabling future simulations for populations for which no past data were available.

Table 12. Descriptions of variables used to model RCW population growth. Variables marked with an asterisk were not included in the primary model-selection, but were tested after selecting a best model from the other variables.

Variable Type	Description	Variable Forms
Growth rate *r*	Ln(population size at time *t*+1 / population size at time *t*) , where population size is in terms of active clusters (territories)	1) Single form
Recruitment Clusters	Number of new recruitment clusters installed, scaled as proportion of population size (active clusters); a recruitment cluster is a group of artificial cavities installed in unoccupied but suitable habitat	1) Single-year value 2) Single-year value, square root transformed 3) Three-year average 4) Three-year average, square root transformed
Cavity Management	Number of active clusters where artificial cavities were installed to maintain a certain number (often 4 or 5) of suitable cavities per cluster. Scaled to population size	1) Single-year value 2) Single-year value, square root transformed 3) Three-year average 4) Three-year average, square root transformed
Midstory Treatment – Fire (a) – Any means (b)	(a) Number of active clusters treated for midstory control with fire (b) Number of active clusters treated for midstory control with any means, including fire, herbicides, mechanical treatment, etc. All scaled to population size	1) Single-year value 2) Single-year value, square root transformed 3) Three-year average 4) Three-year average, square root transformed
Dominant Pine Species	Species constituting 75% or more of the pine > 10" dbh; if no single species constituted 75% of the pine habitat, the top two in order of abundance	1) Single dominant pine species 2) Dominant pine community; single species or top two in order of abundance if no single species reached 75% threshold
Translocation	Number of birds moved into population, scaled to population size. Only applied to populations with < 30 active clusters.	1) Single year value, straight-line relationship
Spatial configuration	Ripley's K calculated for active clusters, only applies to populations with > 29 active clusters.	1) 3 km numerical value 2) 3 km "random" or "clustered" 3) 6 km numerical value 4) 6 km "random" or "clustered"
*Flying Squirrel Removal – # Squirrels (a) – # Clusters (b)	(a) Number of flying squirrels removed (b) Number of clusters from which flying squirrels were removed	1) Single-year value, from active clusters 2) Single-year value, from clusters of any activity status 3) Three-year average, from active clusters 4) Three-year average, from clusters of any activity status 5) Binary variable of whether any squirrel removal occurred in a year
*Storms	Binary variable (0 or 1) whether or not a storm occurred	1) Any tropical storm, tropical depression or hurricane 2) Category 2 or stronger hurricane 3) Category 4 or stronger hurricane

Table 13. Model outputs from the top model for population growth in small populations (6-29 active clusters). The reference category for Dominant Pine is ‘Longleaf.’

<table>
<tr><td colspan="2">Parameter</td><td>Estimate</td><td>Standard Error</td></tr>
<tr><td colspan="2">Intercept</td><td>-0.028</td><td>0.022</td></tr>
<tr><td colspan="2">√ Recruitment Clusters (3-Yr Avg)</td><td>0.075</td><td>0.031</td></tr>
<tr><td colspan="2">√ Cavity Management (3-Yr Avg)</td><td>0.050</td><td>0.026</td></tr>
<tr><td colspan="2">√ Midstory Treatment – Any Method</td><td>0.050</td><td>0.022</td></tr>
<tr><td colspan="2">Dominant Pine - Loblolly</td><td>0.009</td><td>0.016</td></tr>
<tr><td colspan="2">Dominant Pine - Slash</td><td>-0.041</td><td>0.023</td></tr>
<tr><td colspan="2">Dominant Pine - Shortleaf</td><td>-0.058</td><td>0.034</td></tr>
<tr><td colspan="2">Translocation</td><td>0.115</td><td>0.023</td></tr>
<tr><td colspan="4"></td></tr>
<tr><td>Residual Std Dev</td><td>0.1369</td><td># Observations</td><td>458</td></tr>
<tr><td>Population Random Effect Std Dev</td><td>0</td><td># Populations</td><td>53</td></tr>
<tr><td>R^2</td><td>0.167</td><td colspan="2"></td></tr>
</table>

Table 14. Model outputs from the top model for population growth in medium populations (30-75 active clusters).

<table>
<tr><td colspan="2">Parameter</td><td>Estimate</td><td>Standard Error</td></tr>
<tr><td colspan="2">Intercept</td><td>-0.018</td><td>0.021</td></tr>
<tr><td colspan="2">Recruitment Clusters (3-Yr Avg)</td><td>0.167</td><td>0.073</td></tr>
<tr><td colspan="2">√ Midstory Treatment – Fire (3-Year Avg)</td><td>0.063</td><td>0.036</td></tr>
<tr><td colspan="4"></td></tr>
<tr><td>Residual Std Dev</td><td>0.063</td><td># Observations</td><td>233</td></tr>
<tr><td>Population Random Effect Std Dev</td><td>0.008</td><td># Populations</td><td>33</td></tr>
<tr><td>R^2</td><td>0.072</td><td colspan="2"></td></tr>
</table>

Table 15. Model outputs from the top model for population growth in large populations (>75 active clusters). The reference category for Spatial Configuration is ‘Clustered’

<table>
<tr><td colspan="2">Parameter</td><td>Estimate</td><td>Standard Error</td></tr>
<tr><td colspan="2">Intercept</td><td>0.023</td><td>0.008</td></tr>
<tr><td colspan="2">Recruitment Clusters</td><td>0.036</td><td>0.095</td></tr>
<tr><td colspan="2">Cavity Management (3-Yr Avg)</td><td>0.039</td><td>0.033</td></tr>
<tr><td colspan="2">Spatial Configuration – Random</td><td>-0.014</td><td>0.010</td></tr>
<tr><td colspan="4"></td></tr>
<tr><td>Residual Std Dev</td><td>0.037</td><td># Observations</td><td>223</td></tr>
<tr><td>Population Random Effect Std Dev</td><td>0.012</td><td># Populations</td><td>23</td></tr>
<tr><td>R^2</td><td>0.171</td><td colspan="2"></td></tr>
</table>

The response variable for the linear mixed effects model was the intrinsic growth rate *r* between consecutive years for small, medium, and large populations in the form:

$$r = \alpha + \mathrm{a} + \beta_i * covariate_i + \varepsilon$$

where *r* represents the predicted growth rate, α represents the intercept growth rate, *a* represents the population random effect, $\beta i * covariate_i$ describes the effect of habitat and management covariates, and ε represents random stochastic error. For each variable type (Table 12), we first fit univariate mixed effects models (all included a random intercept for each population) and compared each form of the variable type with AIC. Best forms of each variable type then advanced to the second stage, where all possible combinations of best-form variables were compared to select a single best model. We performed this procedure first on the complete data set to separate the data into population size classes, and then performed the 2-step model-selection within each size class.

For past growth rate of small populations, the best AIC model included effects of number of new recruitment clusters (recruitment clusters), number of new artificial cavities in previously existing clusters (cavity management), midstory treatments by prescribed fire or mechanical methods (midstory any method), number of RCWs translocated into the population, and dominant pine type (Table 13). Translocation had the greatest management effect on growth. For medium populations, recruitment clusters and midstory treatments by prescribed fire were significant management covariates (Table 14). The best model for large populations included recruitment clusters, cavity management, and spatial configuration of active clusters (Table 15). In all cases, effects of recruitment clusters, cavity management, midstory treatment and translocation were positive. Greater spatial aggregation of clusters promoted population growth. AIC model data for small, medium, and large populations are provided in Appendix 7. More detailed information on modeling for past and future conditions is provided in Appendix 2.

Future Simulation Model

Best fit linear models of past population growth for small, medium, and large populations were used to stochastically simulate demographic populations beginning with their initial current population size for 25 years under Manager's, (97 populations), Low (96), Medium (96), and High (96) management scenarios. The 25-year future interval was selected because estimating future management treatments by biologists and managers in our elicitations was a challenging task, with increasing uncertainty with time due to future funding, management resources, and habitat and population conditions. Also, results of initial simulations for model planning and development indicated wide variation in the size of simulated populations at 25 years, that would increase further at longer intervals. Current population sizes were based on actual surveys during 2015 to 2017. Each population was simulated with 5,000 replicate runs during the 25-year period. When a population increased or decreased during a simulation from one size-class and model to another, the population size-class model changed accordingly. Stochasticity was created during each 1-year time step by randomly sampling from the probability distribution of applicable model parameters in each scenario. Scenarios were selected to characterize effects of management and model uncertainty for this highly conservation reliant species. Values for model management covariates varied depending on the management scenario.

The future simulation model does not adequately account for all impacts of hurricanes, particularly major storms of less frequent occurrence than more frequent smaller storms. The past population model included effects of hurricanes and other storms during the 1998-2017 period to the extent of causing any annual variation in growth to affected populations. The location of these storms did not impact all populations. Similarly, the intensity of storms were not the same at affected populations. Furthermore, effects of Hurricane Michael as a major category 4 hurricane in 2018 to the Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest and other populations were not included in the past population model. The threat to future viability resulting from the frequency and intensity of hurricanes to particular populations, and projected increases in the frequency of major storms due to climate change must be assessed by other means as discussed in Chapter 5.

Scenarios

Future values of significant habitat and management model covariates for the Manager's scenario were obtained by elicitations to property biologists, foresters, and managers. Personnel estimated the most likely annual future number of recruitment clusters, artificial cavities, prescribed fire treatments, and other management parameters at 5-year intervals for the 25-year period. For instance, responses included the average annual number of new recruitment clusters to be installed, percent of active clusters to receive artificial cavities, and number or percentage of active clusters to be treated by prescribed fire or by any means in future 5-year intervals. Estimating future habitat and management conditions is not certain, which required consideration of future organizational resources for staff, funding and other support to conduct RCW and associated forest management. Biologists and managers responded to our elicitations with their future management estimates assuming the RCW remained a federally listed species and with associated resources, incentives, and related factors to continue species-specific management.

For the Low scenario, values for each management covariate were set to zero. This does not, however, reflect no management or the absence of any RCW conservation management. All populations in the past model are actively managed to some degree, and thus some baseline level of management occurs in all models affecting actual growth and in simulations in the Low scenario. Also, growth will still occur for many populations in this scenario with zero values for management parameters because these parameters in best fit models do not account for all variation in growth. We assume that managers continue to provide nesting and foraging habitat, that is, they implement forest / ecosystem management. Our models therefore cannot estimate the effects of fire suppression and forest practices that led to the decline of the RCW and caused it to become endangered. Adverse impacts of these practices is well documented, and it is clear that a return to them would lead to extirpation of populations and the species. Effective ecosystem management will be necessary in perpetuity if the RCW is to persist. The Low scenario estimates the impact of eliminating vital single species management techniques designed specifically for RCWs, and thus relying on ecosystem management alone. Single species management in this context includes the provisioning of artificial cavities, priority forest habitat restoration treatments to control excessive midstory hardwoods, thinning overstocked and unsuitable stands, strategic spatial placement of recruitment clusters to reduce fragmentation, and other measures specifically to sustain and increase RCWs.

Ecosystem management is the broad concept of management treatments to restore and sustain respective forest communities and ecosystems that have been degraded, damaged, or destroyed with respect to health, integrity and sustainability (Society for Ecological Restoration Science and Policy Working Group 2002). No past or current RCW populations occur in forests that have been restored to a condition of composition and structure where prescribed fire, with few other treatments, would sustain desired ecosystem conditions and this species. Many decades are required to attain a desired future ecosystem condition in which RCWs are no longer dependent on artificial cavities and related special treatments. The Low future scenario will overestimate future population performance because desired ecosystem conditions and management do not exist now or in the reasonably foreseeable future.

Management covariate parameters for the Medium and High scenarios were derived from the distribution of these values in past model data. For the Medium scenario, the overall median from all population means of each management parameter was used as the fixed input value. The Medium scenario represents population projections based on the assumption that the management employed over the past 20 years will continue for the next 25 years. For the High scenario, values of future management parameters were visually selected from the approximate 90th percentile from all combined populations for each size-class model. The High scenario represents projections of what might potentially be achieved should the species be systematically managed more intensively across its range than it has been in the past.

Limits to population growth and size

Population size was limited in any simulation and scenario by carrying capacity. Values for each population were acquired from property and population managers who estimated carrying capacity for their populations at the end of the 25-year period. Carrying capacity reflected the estimated future amount of nesting and foraging habitat, and whether a potential increase in active territories to capacity was the result of recruitment clusters, budding, or pioneering. We imposed a lower bound so that once a population declined below six active clusters it never recovered during the affected replicate 25-year run. If a population declined to this quasi-extirpation threshold, it remained fixed at that final size for all subsequent years under the replicate run. In reality, when an RCW population with adequate monitoring dips that low, if not sooner, successful managers of properties for RCW conservation and recovery would be expected to respond with intensive recovery efforts to prevent extirpation. These management actions may include extensive cavity replacements, habitat restoration, and translocation. However, we chose to model our management scenarios without such intensive rescue efforts for very small populations to illustrate what would be expected if each management scenario continued without significant modification for the entire 25-year period. This lower threshold also corresponds with the minimum population size simulated.

Merging Populations

Separate demographic populations within the same property, or on adjacent properties, were allowed to increase and merge to establish a new and larger demographic population during the future simulation period if predicted by property managers in response to our elicitation. Our elicitation package included maps of the location of current demographic populations and active clusters based on the most current GIS. Managers provided a most likely estimate of time to merging, bounded by estimates of the earliest possible and latest possible years, if a demographic merger was predicted by future growth. To merge, separate demographic populations were expected to increase in population size and at sites where, when united, active clusters were within 6 km (3.7 miles) of a nearest neighbor active territory.

We applied the earliest possible merge year to the High management scenario, the latest possible merge year to the Low scenario, and the manager's estimated merger year to the Medium and the Manager's scenarios. The earliest year for the High scenario was selected because of greater anticipated population growth rates and management. The latest year for the Low Management Scenario represented minimal management with lower expected growth rates.

Although we did not model populations with fewer than six current active clusters, there were four instances where a very small population was predicted to merge with a larger simulated population. In these cases, at the year of merging for each scenario we added the initial population size of the very small population to the larger one, and merged the model inputs under the conservative assumption that the very small population neither increased nor decreased during the intervening time before merging.

Future Simulation Outputs

The following output (Appendix 3 and Appendix 4) was extracted from simulation results at 5-year intervals for each scenario: mean population size, median population size, range of population sizes, non-parametric 95% CIs around the mean population size (constructed by bounding the middle 95% of simulation runs), percent of 5,000 simulation runs ending at 95% or greater of carrying capacity, percent of simulation runs stable or increasing (final population size greater than or equal to the initial size), percent of simulation runs with population sizes under 30 (a threshold that triggers increased management), and the percent of simulation runs quasiextirpated (fell below 6 active clusters). We also calculated a constant growth rate based on median population sizes for the 25-year period for each population, or for the appropriate years when multiple populations merged during the 25-year simulation. Appendix 5 lists for each future management scenario the populations by descending median 25-year population size, with the initial and final resilience size-class, growth rate category, and growth rate. In Appendix 6, future simulated populations are listed by rank descending median population size, resilience size-class, and growth rate under the Manager's scenario with comparisons to the same output from the Low, Medium, and High management future scenarios. Below, we summarize the results for the 25-year simulations of each of the scenarios.

Manager's Scenario

Under the Manager's scenario, there are 84 demographic populations at the end of the 25- year simulation period. The predicted resilience based on median population size and number of populations by resilience categories at the end of the 25-year simulations are: very high (5); high (7); moderate (12); low (36); very low (24). Of those 84 populations, 48 display stable growth rates, 11 negative growth, and 25 increasing growth. The resilience of two populations (Fort Stewart, Francis Marion National Forest-Bonneau Ferry-Santee Coastal Reserve WMA) increased from the current high to a future very high resilience, six populations (Carolina Sandhills NWR-Sandhills State Forest-Cheraw State Park, Fort Polk –Vernon Unit Kisatchie National Forest, Sam Houston National Forest X, Osceola National Forest, Homochitto National Forest, Blackwater River State Forest E–Conecuh National Forest A) changed from the current moderate to high resilience, and nine populations (Savannah River X, Ouachita National Forest X, Croatan National Forest, Chickasawhay District DeSoto National Forest, Big Cypress National Preserve A, Marine Corp Base Camp Lejeune B, Withlacoochee State Forest Citrus, Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge, Georgia Safe Harbor) increased from low to moderate resilience compared to current conditions (Appendix 5, Table A5.1). The Palmetto-Peartree Preserve Complex population in northeastern North Carolina could not be modeled, but may be assumed to represent a 13th moderately resilient population based on current condition.

Resilience: Very High

Table 16 summarizes all populations in the "very high" resilience class in the Manager's scenario, rank ordered based on population growth rate. All populations are predicted to have a stable growth rate with management. The median future size of all five of these populations is at or very near carrying capacity. All populations are managed by federal or state agencies, with the exception of the North Carolina Sandhills population that includes spatially critical RCWs on private lands. Most of the North Carolina Sandhills population resides on Fort Bragg to the northeast and the Sandhills Gamelands (North Carolina Wildlife Resources Commission) and Camp Mackall to the southwest. Private landowners currently enrolled in the Safe Harbor program provide important voluntary and beneficial management that demographically connects the eastern and western sections of this population. Future simulations of this population assume, as for public agencies, that these private landowners will continue to (voluntary) implement beneficial management to sustain these RCWs.

Table 16. Population resilience summary for the “very high” category for the Manager’s scenario. Populations are sorted by rank based on descending λ.

Manager's Future Management Scenario							
Code	Capacity	Ecoregion	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	1312	EGCP	Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest	858	1270	1.016	Very High
1	622	SACP	Fort Stewart	482	622	1.010	Very High
1	893	SH	North Carolina Sandhills	781	893	1.005	Very High
1	540	MACP	Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA	496	540	1.003	Very High
1	550	EGCP	Eglin Air Force Base	504	540	1.003	Very High

Resilience: High

Of the seven populations in the high resilience category, four are projected to have an increasing growth rate and three a stable trend (Table 17). Except for the Fort Polk-Vernon Unit Kisatchie National Forest population, all populations increase to attain carrying capacity. The simulated predicted median future population size (315) of the Fort Polk-Vernon Unit Kisatchie National Forest is less than its capacity. The Sam Houston National Forest X population is established by a demographic merger of the current Sam Houston National Forest A and Sam Houston National Forest B populations at year 18. A severe outbreak of southern pine beetles on the Homochitto National Forest occurred after the model and simulations were completed. National Forest personnel have been implementing beetle control measures, but the number of active clusters potentially lost has not yet been determined.

Table 17. Population resilience summary for the “high” category in the Manager’s scenario. Populations are sorted by rank descending λ.

Manager's Future Management Scenario							
Code	Capacity	Ecoregion	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	324	EGCP	Blackwater River State Forest E-Conecuh National Forest A	138	324	1.035	High
1	300	SACP	Osceola National Forest	152	300	1.028	High
1	422	SH	Carolina Sandhills NWR-Sandhills State Forest-Cheraw State Park	248	416	1.021	High
1	254	EGCP	Homochitto National Forest	151	251	1.021	High
1	429	WGCP	Fort Polk-Vernon Unit Kisatchie National Forest	223	315	1.014	High
1	410	SH	Fort Benning	386	410	1.002	High
2	256	UWGCP	Sam Houston National Forest X	249	256	1.001	High

Resilience: Moderate

Twelve populations with a median size from 110 to 211 active clusters are in the future moderate resilience class (Table 18). Three of these populations are formed by a demographic merger of two or more smaller populations (Savannah River X, Ouachita National Forest X, and Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge). Eight of the 12 populations in this category are projected to have an increasing growth rate, and the other four a stable trend. Three populations increase to reach carrying capacity (Marine Corps Base Camp Lejeune B, Withlacoochee State Forest Citrus, and Evangeline Unit Kisatchie National Forest-Alexander State Forest). The Oakmulgee District A Talladega National Forest and Croatan National Forest populations increase to close to carrying capacity. The Georgia Safe Harbor population is a significant population residing on private lands in the Red Hills region. The limited future growth of this population was based on capacity estimates and growth primarily by budding and pioneering, in contrast to recruitment clusters, estimated by program managers. Of all future populations in this resilience class, only three (Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge, Savannah River X, and Bienville National Forest A) have a future estimated capacity greater than 249 active clusters and thus could potentially reach High resilience with sufficient growth.

Table 18**.** Population resilience summary for the "moderate" category for the Manager's scenario. Populations are sorted by rank based on descending λ.

Manager's Future Management Scenario							
Code	Capacity	Ecoregion	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
2	255	WGCP	Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge	137	157	1.031	Moderate
2	315	SACP	Savannah River X	130	185	1.025	Moderate
2	140	OM	Ouachita National Forest X	91	124	1.025	Moderate
1	225	UEGCP	Oakmulgee District A Talladega National Forest	114	210	1.025	Moderate
1	138	MACP	Croatan National Forest	69	127	1.025	Moderate
1	385	UEGCP	Bienville National Forest A	117	211	1.024	Moderate
1	155	EGCP	Chickasawhay District DeSoto National Forest	69	120	1.022	Moderate
1	200	FP	Big Cypress National Preserve A	83	143	1.022	Moderate
1	144	MACP	Marine Corps Base Camp Lejeune B	89	142	1.019	Moderate
1	120	FP	Withlacoochee State Forest Citrus	82	116	1.014	Moderate
1	180	WGCP	Evangeline Unit Kisatchie National Forest-Alexander State Forest	152	177	1.006	Moderate
1	110	EGCP	Georgia Safe Harbor	97	110	1.005	Moderate

Resilience: Low

The median simulated future size of the 36 populations in the low resilience category range from 34 to 97 active clusters (Table 19). Twelve populations are projected to have an increasing growth rate, 23 a stable trend, and one a decreasing growth rate. Populations with stable or positive growth rates reflect effects of beneficial conservation management in populations with inherently low resilience. Five populations within the low resilience class are formed by a merger of two or more smaller populations (Angelina National Forest X, Winn District Kistachie National Forest X, Sabine National Forest X, Catahoula X Kistachie National Forest, and Sam D.

Hamilton Noxubee NWR X). Sixteen populations are at carrying capacity as a consequence of growth or the initial population size. Seven populations have sufficient capacity, if they continue to grow beyond the 25 years projected, to potentially transition to the moderately resilient class.

Table 19. Population resilience summary for the "low" category for the Manager's scenario. Populations are sorted by rank based on descending λ. Populations with yellow highlight are at or near carrying capacity.

Manager's Future Management Scenario							
Code	Capacity	Ecoregion	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	39	CRV	Talladega	14	39	1.042	Low
1	96	SH	Fort Gordon	24	62	1.039	Low
1	53	FP	Bull Creek-Triple N WMA	18	43	1.036	Low
1	75	CRV	Shoal Creek District-Talladega National Forest	23	53	1.034	Low
1	93	EGCP	Conecuh National Forest B	25	57	1.034	Low
1	35	WGCP	Angelina National Forest A	13	35	1.032	Low
1	145	EGCP	DeSoto District DeSoto National Forest A	47	86	1.024	Low
1	50	FP	Corbett WMA	30	47	1.024	Low
1	60	UWGCP	Sabine National Forest A	32	57	1.023	Low
1	40	FP	Ocala National Forest B	20	34	1.022	Low
1	82	UEGCP	Bienville National Forest B	25	42	1.021	Low
1	97	FP	Ocala National Forest C	40	66	1.020	Low
1	44	UWGCP	Davy Crockett National Forest B	25	40	1.019	Low
1	71	FP	Avon Park Air Force Range	35	55	1.019	Low
2	125	WGCP	Angelina National Forest X	67	96	1.018	Low
1	70	SH	Fort Jackson	41	65	1.018	Low
1	133	EGCP	DeSoto District DeSoto National Forest B	53	79	1.016	Low
1	61	MACP	Marine Corps Base Camp Lejeune A	33	49	1.016	Low
2	155	WGCP	Winn District Kisatchie National Forest X	69	87	1.016	Low
1	45	EGCP	Silver Lake WMA	31	44	1.014	Low
2	65	UWGCP	Sabine National Forest X	44	54	1.014	Low
1	93	FP	Ocala National Forest A	58	93	1.014	Low
1	45	EGCP	Jones Ecological Research Center	32	44	1.013	Low
1	65	FP	Three Lakes WMA	45	59	1.011	Low
2	216	WGCP	Catahoula X Kisatchie National Forest	67	78	1.010	Low
1	75	UWGCP	Davy Crockett National Forest A	59	72	1.008	Low
1	40	SACP	Camp Blanding	31	38	1.008	Low
1	39	SH	Manchester Poinsett	32	38	1.006	Low
1	160	P	Piedmont NWR-Oconee National Forest-Hithchiti Experimental Forest	83	97	1.006	Low
1	40	UWGCP	Sam Houston National Forest F	35	40	1.005	Low
1	46	FP	Withlacoochee State Forest Croom	39	44	1.005	Low
1	52	FP	Babcock Webb WMA	45	51	1.005	Low
1	40	MACP	Holly Shelter Game Land	36	40	1.004	Low
2	49	UEGCP	Sam D. Hamilton Noxubee NWR X	41	46	1.003	Low
1	100	SACP	Brosnan Forest	86	92	1.003	Low
1	36	UWGCP	Felsenthal-TNC	35	34	0.999	Low

Resilience: Very Low

Of the 24 populations in this category, only two are projected to have increasing growth rates, 12 to be stable, and 10 to have decreasing growth rates (Table 20). As for populations in the low resilience category, the stable and increasing populations with inherently very low resilience reflect the estimated effects of successful and intensive conservation management. Many of these populations have been recipients of RCW translocation to augment population size and growth. All of the populations within this resilience class require intensive management. Capacity limitations for most of these populations restrict their future size as small populations within this resilience category. Only seven of these 24 populations have a 25-year capacity of more than 30 active clusters to potentially transition, with additional growth, to the low resilience category. One population in the in the very low resilience class (Picayune Strand State Forest X) is formed due to a merger of two smaller populations. Without intensive management, these populations are highly likely to be extirpated (e.g., Picayune Strand).

Table 20. Population resilience summary for the “very low” category for the Manager’s scenario. Populations are sorted by rank based on descending λ.

Manager's Future Management Scenario							
Code	Capacity	Ecoregion	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	33	UEGCP	Bienville National Forest C	10	25	1.038	Very Low
1	30	SACP	Webb Wildlife Center	14	29	1.030	Very Low
1	23	FP	St. Sebastian River Preserve State Park	13	21	1.019	Very Low
1	20	UWGCP	Warren Prairie Natural Area	13	20	1.017	Very Low
1	21	MACP	Piney Grove	14	21	1.016	Very Low
1	23	FP	Babcock Ranch Preserve	12	17	1.015	Very Low
1	47	WGCP	Catahoula A Kisatchie National Forest-Winn Kisatchie National Forest	12	17	1.014	Very Low
1	20	UWGCP	Sam Houston National Forest D	15	20	1.011	Very Low
1	13	FP	TNC Disney Wilderness Preserve	9	12	1.011	Very Low
1	24	MACP	Military Ocean Terminal Supply Point	20	23	1.005	Very Low
1	30	FP	Dupuis Wildlife and Environmental Area	15	18	1.004	Very Low
1	26	WGCP	Crowell Lumber	21	23	1.004	Very Low
1	10	FP	Platt Branch Wildlife and Environmental Area	6	6	1.000	Very Low
1	19	EGCP	St. Marks NWR B	6	6	1.000	Very Low
1	20	MACP	Yawkey Wildlife Center	14	14	0.999	Very Low
1	15	MACP	Lewis Ocean Bay Heritage Preserve	12	11	0.998	Very Low
1	8	MACP	Longleaf Heritage Preserve - Lynchburg Savanna Heritage Preserve WMA	8	6	0.989	Very Low
1	9	SACP	Okefenokee NWR C	9	6	0.984	Very Low
1	45	OM	McCurtain County Wilderness Area	15	9	0.980	Very Low
1	14	SACP	Okefenokee NWR A	11	6	0.976	Very Low
1	27	GCPM	Big Branch Marsh NWR	20	10	0.973	Very Low
2	25	FP	Picayune Strand State Forest X	16	12	0.970	Very Low
1	34	SACP	Okefenokee NWR D	13	6	0.970	Very Low
1	29	SACP	Okefenokee NWR B	15	6	0.964	Very Low

Medium Management Scenario

As with the Manager’s scenario, under the Medium management scenario there are 84 demographic populations at the end of the 25-year simulation period. The predicted resilience based on median population size and number of populations by resilience categories at the end of the 25-year simulations are: very high (5); high (7); moderate (13); low (38); very low (21). Of those 84 populations, 32 display increasing growth, 50 stable growth rates, and two negative rates. Among the future scenarios, results of the Medium and Manager’s are most similar (Figure 27). These similarities reflect the extent future management predicted by biologists and managers for the Manager’s scenario, as parameters in the best models, are comparable to the average and median parameter values used in the Medium scenario. Property managers and biologists provided relatively conservative estimates for future management comparable to overall average past treatments from all populations, relative to more extreme values as in the Low and High scenarios. Compared to the Manager’s scenario, the Medium scenario projects one additional population of moderate resilience, two more populations of low resilience, and three fewer populations with very low resilience . Differences between the total number of populations simulated in Medium scenario (80) and Manager’s scenario (84) reflect different patterns of demographic merging among initial populations.

Figure 27. Number of populations by resilience category for past-to-current condition and future management scenarios.

Resilience: Very High

The five populations in the very high resilience category (Table 21) are identical to those for the Manager's Expectation scenario, of which all are predicted to have a stable growth rate. Growth rates are limited by carrying capacity, and the future median size of all populations is at or near carrying capacity (Table 17). The Fort Polk-Vernon Unit Kisatchie National Forest populations is the only population that does not increase sufficiently to attain carrying capacity. The Sam Houston National Forest X population, as in the Manager's scenario, is initially near its carrying capacity. None of the populations in the high resilience have the carrying capacity to support more than 499 active clusters as required for populations in the very high resilience category.

Table 21. Population resilience summary for the "very high" category for the Medium management scenario. Populations are sorted by rank based on descending λ.

Medium Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	EGCP	1312	Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest	858	1257	1.015	Very High
1	SH	893	North Carolina Sandhills	781	893	1.005	Very High
1	SACP	622	Fort Stewart	482	622	1.010	Very High
1	EGCP	550	Eglin Air Force Base	504	550	1.004	Very High
1	MACP	540	Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA	496	540	1.003	Very High

Table 22. Population resilience summary for the "high" category for the Medium management scenario. Populations are sorted by rank based on descending λ.

Medium Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	EGCP	324	Blackwater River State Forest E-Conecuh National Forest A	138	324	1.035	High
1	SACP	300	Osceola National Forest	152	300	1.028	High
1	EGCP	254	Homochitto National Forest	151	254	1.021	High
1	SH	422	Carolina Sandhills NWR-Sandhills State Forest-Cheraw State Park	248	411	1.020	High
1	WGCP	429	Fort Polk-Vernon Unit Kisatchie National Forest	223	311	1.013	High
1	SH	410	Fort Benning	386	410	1.002	High
2	UWGCP	256	Sam Houston National Forest X	246	256	1.001	High

Resilience: High

Future populations with high resilience are the same as those in the Manager's scenario (Table 22). The Sam Houston National Forest X population, as in the Manager's scenario, is initially near its carrying capacity. None of the populations with high resilience have the carrying capacity to support more than 499 active clusters as minimally required to advance to the very high resilience class.

Resilience: Moderate

The 13 populations in the moderate resilience class (Table 23) include the same 12 populations with moderate resilience in the Manager's scenario (Table 18), and in addition the Piedmont NWR-Oconee National Forest-Hithchiti Experimental Forest. Three populations (Savannah River X, Ouachita National Forest X and Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge) are established by the demographic merger of two or more smaller populations. Eight populations are projected to have an increasing growth rate and five are stable. As for populations with moderate resilience in the Manager's scenario, three populations in the Medium scenario increase to reach carrying capacity (Marine Corps Base Camp Lejeune B, Withlacoochee State Forest Citrus, and Evangeline Unit Kisatchie National Forest-Alexander State Forest). The Oakmulgee District A Talladega National Forest and Croatan National Forest populations increase to close to carrying capacity.

Table 23**.** Population resilience summary for the "moderate" category for the Medium management scenario. Populations are sorted by rank based on descending λ.

Medium Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	UEGCP	385	Bienville National Forest A	117	239	1.029	Moderate
2	SACP	315	Savannah River X	126	181	1.027	Moderate
2	OM	140	Ouachita National Forest X	91	126	1.026	Moderate
2	WGCP	255	Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge	131	146	1.026	Moderate
1	EGCP	155	Chickasawhay District DeSoto National Forest	69	131	1.026	Moderate
1	MACP	138	Croatan National Forest	69	127	1.025	Moderate
1	UEGCP	225	Oakmulgee District A Talladega National Forest	114	201	1.023	Moderate
1	FP	200	Big Cypress National Preserve A	83	146	1.023	Moderate
1	FP	120	Withlacoochee State Forest Citrus	82	115	1.014	Moderate
1	P	160	Piedmont NWR-Oconee National Forest-Hithchiti Experimental Forest	83	101	1.008	Moderate
1	MACP	144	Marine Corps Base Camp Lejeune B	89	142	1.007	Moderate
1	WGCP	180	Evangeline Unit Kisatchie National Forest-Alexander State Forest	152	175	1.006	Moderate
1	EGCP	110	Georgia Safe Harbor	97	110	1.005	Moderate

Resilience: Low

Table 24 summarizes all populations classified as "low" resilience, rank ordered based on population growth rate. The five populations in this category established by a demographic merger of two or more populations are the same as those in the comparable analysis in the Manager's Expectation scenario. Populations with low resilience generally had higher growth rates in the Medium management scenario than in the Manager's scenario. Of the 38 populations with Low resilience, 18 populations are projected to have an increasing growth rate, 20 to be stable, and none to decrease. Median population size ranges from 30 to 91 active clusters across the spectrum of the low resilience category (30 – 99). The population size of 17 populations are at carrying capacity or at 95% of capacity. Five populations have sufficient capacity with additional future growth to transition to the moderate resilience size class: Catahoula X Kisatchie National Forest, Winn District Kisatchie National Forest X, DeSoto District DeSoto National Forest A, DeSoto District DeSoto National Forest B, and Angelina National Forest X. The capacity of the remaining 33 populations is limited to the low resilience class. The overall increasing and stable growth rates for these populations with inherently low resilience is indicative of effective conservation management.

Resilience: Very Low

In this scenario (Table 25), 21 populations are in the very low resilience category, compared to 24 populations in the Manager's scenario (Table 20, Figure 27). As in the Manager's scenario, one population in the very low resilience category is formed by a demographic merger of two smaller populations (Picayune Strand State Forest X). As in the low resilience class, populations with very low resilience generally perform better in the Medium management scenario than in the Manager's Expectation scenario: three had increasing growth rates, 16 were stable, and only two had decreasing rates. Six populations are at or near carrying capacity. Only three populations have the capacity, with additional growth, to transition to the low resilience class: McCurtain County Wilderness Area, Okefenokee NWR D, and Dupuis Wildlife and Environmental Area. The capacity of the remaining 18 populations is restricted to the very low resilience class. The favorable stable and increasing growth rates of these small populations with very low resilience, as in the Manager's scenario, represent effects of successful management.

Table 24. Population resilience summary for the “low” category for the Medium management scenario. Populations are sorted by rank based on descending λ. Populations with yellow highlight are at or near carrying capacity.

Medium Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	WGCP	47	Catahoula A Kisatchie National Forest-Winn Kisatchie National Forest	12	40	1.049	Low
1	UEGCP	33	Bienville National Forest C	10	32	1.048	Low
1	CRV	39	Talladega	14	37	1.040	Low
1	FP	53	Bull Creek-Triple N WMA	18	45	1.037	Low
1	CRV	75	Shoal Creek District-Talladega National Forest	23	51	1.032	Low
1	WGCP	35	Angelina National Forest A	13	34	1.032	Low
1	UEGCP	82	Bienville National Forest B	25	54	1.031	Low
1	SH	96	Fort Gordon	24	52	1.031	Low
1	SACP	30	Webb Wildlife Center	14	30	1.031	Low
1	EGCP	93	Conecuh National Forest B	25	53	1.031	Low
1	FP	40	Ocala National Forest B	20	39	1.027	Low
1	EGCP	145	DeSoto District DeSoto National Forest A	47	87	1.025	Low
1	FP	97	Ocala National Forest C	40	71	1.023	Low
1	UWGCP	60	Sabine National Forest A	32	56	1.023	Low
1	SH	39	Manchester Poinsett	32	38	1.022	Low
1	FP	71	Avon Park Air Force Range	35	60	1.021	Low
1	FP	50	Corbett WMA	30	47	1.021	Low
1	UWGCP	44	Davy Crockett National Forest B	25	42	1.021	Low
1	MACP	61	Marine Corps Base Camp Lejeune A	33	57	1.019	Low
2	UWGCP	65	Sabine National Forest X	49	60	1.019	Low
1	SH	70	Fort Jackson	41	64	1.018	Low
1	EGCP	133	DeSoto District DeSoto National Forest B	53	82	1.018	Low
1	FP	93	Ocala National Forest A	58	85	1.015	Low
2	WGCP	125	Angelina National Forest X	64	85	1.015	Low
2	WGCP	155	Winn District Kisatchie National Forest X	70	87	1.014	Low
1	EGCP	31	Silver Lake WMA	31	44	1.014	Low
1	EGCP	45	Jones Ecological Research Center	32	44	1.013	Low
1	FP	65	Three Lakes WMA	45	60	1.011	Low
2	WGCP	216	Catahoula X Kisatchie National Forest	75	91	1.011	Low
1	SACP	40	Camp Blanding	31	39	1.009	Low
1	UWGCP	75	Davy Crockett National Forest A	59	73	1.008	Low
2	UEGCP	49	Sam D. Hamilton Noxubee NWR X	41	47	1.008	Low
1	FP	46	Withlacoochee State Forest Croom	39	45	1.006	Low
1	UWGCP	40	Sam Houston National Forest F	35	39	1.005	Low
1	FP	52	Babcock Webb WMA	45	51	1.005	Low
1	SACP	100	Brosnan Forest	86	96	1.004	Low
1	MACP	40	Holly Shelter Game Land	36	39	1.003	Low
1	UWGCP	36	Felsenthal-TNC	35	36	1.001	Low

Table 25. Population resilience summary for the “very low” category for the Medium management scenario. Populations are sorted by rank based on descending λ. Populations with yellow highlight are at or near carrying capacity.

Medium Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	FP	23	Babcock Ranch Preserve	12	23	1.026	Very Low
1	SACP	34	Okefenokee NWR D	13	23	1.023	Very Low
1	FP	23	St. Sebastian River Preserve State Park	13	23	1.023	Very Low
1	UWGCP	20	Warren Prairie Natural Area	13	20	1.017	Very Low
1	FP	30	Dupuis Wildlife and Environmental Area	15	24	1.016	Very Low
1	MACP	21	Piney Grove	14	21	1.016	Very Low
1	SACP	29	Okefenokee NWR B	15	22	1.015	Very Low
1	FP	13	TNC Disney Wilderness Preserve	9	13	1.014	Very Low
1	MACP	20	Yawkey Wildlife Center	14	20	1.014	Very Low
1	UWGCP	20	Sam Houston National Forest D	15	20	1.012	Very Low
1	MACP	15	Lewis Ocean Bay Heritage Preserve	12	15	1.009	Very Low
1	WGCP	26	Crowell Lumber	21	26	1.009	Very Low
1	MACP	24	Military Ocean Terminal Supply Point	20	24	1.007	Very Low
1	OM	45	McCurtain County Wilderness Area	15	18	1.007	Very Low
1	GCPM	27	Big Branch Marsh NWR	20	22	1.004	Very Low
2	FP	25	Picayune Strand State Forest X	18	20	1.002	Very Low
1	SACP	14	Okefenokee NWR A	11	11	1.001	Very Low
1	FP	10	Platt Branch Wildlife and Environmental Area	6	6	1.000	Very Low
1	EGCP	19	St. Marks NWR B	6	6	1.000	Very Low
1	SACP	9	Okefenokee NWR C	9	9	0.998	Very Low
1	MACP	8	Longleaf Heritage Preserve - Lynchburg Savanna Heritage Preserve WMA	8	6	0.990	Very Low

Low Management Scenario

Under the Low Management Scenario, there are 81 demographic populations at the end of the 25-year simulation period. The predicted resilience based on median population size and number of populations by resilience categories of the 25-year simulations are: very high (5), high (5), moderate (9), low (12), very low (50). Of those 81 populations, three have increasing growth rates, 20 are stable, and 58 are projected to have declining growth rates. The number and proportion of populations in the very low resilience class increases significantly compared to the Manager's and Medium scenarios (Figure 27). This is mostly a consequence of populations in the very low resilience category that do not increase and transition to the low resilience class as they did in the Manager's and Medium scenarios (Appendix 6). The number of populations in the very high and high resilience categories (10) is less than in the Medium (12) and Manager's (12) scenarios (Figure 27). Most small populations are projected to be in serious risk of extirpation in the low management scenario. Larger stable or increasing populations in this scenario do not necessarily represent persistence in response to long-term poor and insufficient management as the projections assume a baseline level of management. All of these populations remain dependent on effective management with artificial cavities, prescribed fire and silvicultural treatments to restore and sustain suitable foraging and cluster habitat. All of the larger populations available for model development have been successfully managed for RCWs in the past, and thus the presence of larger stable or increasing populations in this scenario reflects the effective past management that got them to this level, as well as their projected performance under low management once at that level. Even though management parameter coefficients (e.g., recruitment clusters, cavity management) in the best fit past models for populations were set to zero for simulations in this scenario, variation in growth still occurs as there are other model sources of variation in growth (e.g., random stochastic error, random population effects, intercepts) besides these management parameters. As previously discussed in this chapter (and Appendix 2), this scenario provides a useful, though limited, comparison of effects of poor management, given that various limitations precluded the development of a model scenario that could accurately portray the absence of management.

Resilience: Very High

Table 26 summarizes all populations that are classified as "very high" resilience in the Low Management scenario, rank ordered based on population growth rate. The five populations in this category are the same as in the Manager's (Table 16) and Medium (Table 21) scenarios. All are predicted to have a stable growth rate, but growth rates are lower than in the Manager's scenario (Table 16). The median future size of the Fort Stewart, North Carolina Sandhills, Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA, and Eglin Air Force Base populations is the same as in the Manager's (Table 16) and Medium (Table 21) scenarios. The Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest population size increases, but the median population size at 25 years is slightly less than in the Manager's and Medium scenarios. All populations except Apalachicola National Forest-St. Marks NWR-

Tate's Hell State Forest attain carrying capacity.

Table 26. Population resilience summary for the “very high” category for the Low management scenario. Populations are sorted by rank based on descending λ.

Low Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	EGCP	1312	Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest	858	1136	1.011	Very High
1	SACP	622	Fort Stewart	482	622	1.010	Very High
1	SH	893	North Carolina Sandhills	781	893	1.005	Very High
1	MACP	540	Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA	496	539	1.003	Very High
1	EGCP	550	Eglin Air Force Base	504	540	1.003	Very High

Resilience: High

In the Low Management scenario (Table 27), five populations are classified as “high” resilience, compared to seven populations in the Manager’s (Table 16) and Medium (Table 21) scenarios. The two populations that are high resilience in the Manager’s and Medium scenarios but not the Low scenario are Homochitto National Forest and Sam Houston X. The Sam Houston X population is created by a demographic merger of Sam Houston National Forest A and Sam Houston National Forest B populations in the Manager’s and Medium scenarios, whereas this merger does not occur in the Low scenario. The Homochitto National Forest population does not increase sufficiently to attain the minimum size class requirement of 250 active clusters required for the high resilience class, although its median population size of 248 active clusters is very near the requirement. Three populations (Blackwater River State Forest E-Conecuh National Forest A, Osceola National Forest, and Fort Benning) increase to either attain carrying capacity or 95% of capacity.

Table 27. Population resilience summary for the “high” category for the Low management scenario. Populations are sorted by rank based on descending λ.

Low Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	EGCP	324	Blackwater River State Forest E-Conecuh National Forest A	138	313	1.033	High
1	SACP	300	Osceola National Forest	152	300	1.028	High
1	SH	422	Carolina Sandhills NWR-Sandhills State Forest-Cheraw State Park	248	371	1.016	High
1	WGCP	429	Fort Polk-Vernon Unit Kisatchie National Forest	223	267	1.007	High
1	SH	410	Fort Benning	386	410	1.002	High

Resilience: Moderate

In the Low Scenario, nine populations are classified as “moderate” resilience (Table 28), compared to 12 populations in the Manager's and 13 in the Medium scenarios (Figure 27). One of these populations is projected to have an increasing growth rate, and the other eight are stable. The Homochitto National Forest population is the only population to increase to a population size (248) within 95% of carrying capacity, and to nearly transition into the high resilience category (250 – 299 active clusters). Six of the nine moderately resilient populations lack adequate population carrying capacity to potentially become highly resilient. The Savannah River X and Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge populations are moderately resilient in the Manager's and Medium scenarios, due to demographic mergers of two or more populations. These two populations are absent from the moderate resilience category in the Low scenario class because their component populations did not increase sufficiently for a demographic merger (Appendix 6). Four other populations of moderate resilience in the Manager's and Medium scenarios do not achieve moderate resilience in the Low scenario due to insufficient growth to transition from the low resilience category (Appendix 6).

Table 28. Population resilience summary for the "moderate" category for the Low management scenario. Populations are sorted by rank based on descending λ.

Low Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	UEGCP	385	Bienville National Forest A	117	205	1.023	Moderate
1	EGCP	254	Homochitto National Forest	151	248	1.020	Moderate
1	FP	200	Big Cypress National Preserve A	83	127	1.017	Moderate
1	UEGCP	225	Oakmulgee District A Talladega National Forest	114	172	1.017	Moderate
1	MACP	144	Marine Corps Base Camp Lejeune B	89	134	1.016	Moderate
1	FP	120	Withlacoochee State Forest Citrus	82	105	1.010	Moderate
1	EGCP	110	Georgia Safe Harbor	97	110	1.005	Moderate
1	WGCP	180	Evangeline Unit Kisatchie National Forest-Alexander State Forest	152	167	1.004	Moderate
2	UWGCP	256	Sam Houston National Forest X	214	214	1.000	Moderate

Resilience: Low

In the Low management scenario, 12 populations are classified as "low" resilience (Table 29) compared to 36 in the Manager's and 38 in the Medium scenarios (Figure 27). With the exception of the Brosnan Forest and Piedmont NWR-Oconee National Forest-Hithchiti Experimental Forest populations, these populations have negative growth rates and are projected to decline from the initial population size. The Ocala National Forest A and Davy Crockett National Forest A populations lack adequate capacity, had there been sufficient positive growth, to become moderately resilient populations (100 – 249 active clusters). All other populations have the carrying capacity to become populations of moderate resilience size class, but declined rather than increasing to this level. Three populations (Croatan National Forest, Ouachita National Forest X, and Chickasawhay District DeSoto National Forest) of moderate resilience in the Manager's and Medium scenarios declined in the Low scenario to become low resilience populations (Appendix 6). The other nine populations in the Low scenario low resilience class were categorized as low future resilience in the Manager's and Medium scenarios as well (Appendix 6), but with declining instead of increasing or stable growth rates as in the other scenarios (Appendix 6).

Table 29. Population resilience summary for the "low" category for the Low management scenario. Populations are sorted by rank based on descending λ.

Low Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	SACP	100	Brosnan Forest	86	89	1.001	Low
1	P	160	Piedmont NWR-Oconee National Forest-Hithchiti Experimental Forest	83	87	1.002	Low
1	EGCP	155	Chickasawhay District DeSoto National Forest	69	55	0.991	Low
2	OM	140	Ouachita National Forest X	66	53	0.986	Low
1	MACP	138	Croatan National Forest	69	45	0.983	Low
1	FP	93	Ocala National Forest A	58	38	0.984	Low
2	WGCP	216	Catahoula X Kisatchie National Forest	49	37	0.984	Low
1	UWGCP	75	Davy Crockett National Forest A	59	37	0.981	Low
2	WGCP	125	Angelina National Forest X	47	35	0.985	Low
1	EGCP	133	DeSoto District DeSoto National Forest B	53	35	0.983	Low
1	EGCP	145	DeSoto District DeSoto National Forest A	47	33	0.985	Low
2	WGCP	155	Winn District Kisatchie National Forest X	37	30	0.987	Low

Resilience: Very Low

In the Low Management scenario, 50 future populations are classified as "very low" inherent or baseline resilience (Table 30). None of these populations has increasing growth, two are stable, and 48 have decreasing growth rates. In the Manager's and Medium scenarios very low resilience category, there are respectively 24 and 21 populations. The much greater number of populations in the Low scenario with very low resilience is a consequence of negative growth rates among most of the populations with low resilience in the Manger's and Medium scenarios (Appendix 6). Although 32 (64%) of the 50 populations with very low resilience have the carrying capacity to support more resilient populations, the decreasing growth rates projected under low management, which represents reduced management compared to current conditions, restricts these populations to the very low resilience category.

Table 30. Population resilience summary for the “very low” category for the Low management scenario. Populations are sorted by rank based on descending λ.

Low Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	FP	10	Platt Branch Wildlife and Environmental Area	6	6	1.000	Very Low
1	EGCP	19	St. Marks NWR B	6	6	1.000	Very Low
1	MACP	61	Marine Corps Base Camp Lejeune A	33	26	0.990	Very Low
1	UWGCP	40	Sam Houston National Forest F	35	27	0.990	Very Low
1	UWGCP	60	Sabine National Forest A	32	25	0.989	Very Low
1	MACP	8	Longleaf Heritage Preserve - Lynchburg Savanna Heritage Preserve WMA	8	8	0.989	Very Low
1	FP	46	Withlacoochee State Forest Croom	39	29	0.988	Very Low
1	FP	97	Ocala National Forest C	40	29	0.987	Very Low
1	UWGCP	36	Felsenthal-TNC	35	25	0.986	Very Low
1	UEGCP	49	Sam D. Hamilton Noxubee NWR X	24	22	0.986	Very Low
1	SH	70	Fort Jackson	41	28	0.985	Very Low
1	UWGCP	44	Davy Crockett National Forest B	25	17	0.984	Very Low
1	EGCP	45	Jones Ecological Research Center	32	21	0.984	Very Low
1	SH	96	Fort Gordon	24	16	0.984	Very Low
1	SACP	9	Okefenokee NWR C	9	6	0.984	Very Low
1	FP	13	TNC Disney Wilderness Preserve	9	6	0.984	Very Low
1	UEGCP	82	Bienville National Forest B	25	17	0.984	Very Low
1	FP	65	Three Lakes WMA	45	29	0.983	Very Low
1	FP	71	Avon Park Air Force Range	35	23	0.983	Very Low
1	EGCP	31	Silver Lake WMA	31	20	0.982	Very Low
1	SH	39	Manchester Poinsett	32	20	0.981	Very Low
1	MACP	40	Holly Shelter Game Land	36	22	0.981	Very Low
1	SACP	40	Camp Blanding	31	19	0.981	Very Low
1	WGCP	20	Angelina National Forest A	13	10	0.980	Very Low
1	UEGCP	33	Bienville National Forest C	10	6	0.980	Very Low
1	SACP	30	Webb Wildlife Center	14	8	0.980	Very Low
1	MACP	21	Piney Grove	14	8	0.979	Very Low
1	UWGCP	20	Sam Houston National Forest D	15	9	0.979	Very Low
1	FP	52	Babcock Webb WMA	45	26	0.978	Very Low
1	WGCP	26	Crowell Lumber	21	12	0.977	Very Low
1	UWGCP	20	Warren Prairie Natural Area	13	7	0.977	Very Low
1	SACP	14	Okefenokee NWR A	11	6	0.976	Very Low
1	WGCP	47	Catahoula A Kisatchie National Forest-Winn Kisatchie National Forest	12	6	0.974	Very Low
1	EGCP	93	Conecuh National Forest B	25	13	0.974	Very Low
1	CRV	75	Shoal Creek District-Talladega National Forest	23	12	0.974	Very Low
1	FP	23	Babcock Ranch Preserve	12	6	0.973	Very Low
1	MACP	15	Lewis Ocean Bay Heritage Preserve	12	6	0.973	Very Low
1	FP	40	Ocala National Forest B	20	10	0.972	Very Low
1	FP	53	Bull Creek-Triple N WMA	18	9	0.971	Very Low
1	SACP	34	Okefenokee NWR D	13	6	0.970	Very Low
1	FP	18	Picayune Strand State Forest B	13	6	0.970	Very Low
1	FP	23	St. Sebastian River Preserve State Park	13	6	0.970	Very Low
1	MACP	24	Military Ocean Terminal Supply Point	20	9	0.969	Very Low
1	CRV	39	Talladega	14	6	0.967	Very Low
1	MACP	20	Yawkey Wildlife Center	14	6	0.967	Very Low
1	OM	45	McCurtain County Wilderness Area	15	6	0.964	Very Low
1	SACP	29	Okefenokee NWR B	15	6	0.964	Very Low
1	FP	30	Dupuis Wildlife and Environmental Area	15	6	0.962	Very Low
1	GCPM	27	Big Branch Marsh NWR	20	6	0.953	Very Low
1	FP	50	Corbett WMA	30	7	0.951	Very Low

High Management Scenario

Under the High Management Scenario, there are 81 demographic populations at the end of the 25-year simulation period. The predicted resilience based on median population size and number of populations by resilience categories are: very high (5), high (9), moderate (17), low (32), very low (18). Compared to all other management scenarios, the performance of future populations with high levels of conservation management is enhanced. Fourteen future population reside in the very high and high resilience classes, and 17 populations are in the moderate resilience category, more than in any other future management scenario (Figure 27). Only 18 populations are in the very low resilience class, a smaller number and proportion than in other management scenarios (Figure 27). Overall, differences in the High management scenario are the consequence of a greater number of populations increasing from their initial size to transition to a more resilient category. The High Management scenario is a close approximation to the maximum resiliency achievable for RCWs given the current land base for conservation and their 25-year carrying capacities.

Resilience: Very High

All five future populations with very high resilience (Table 31) are the same as those for all other scenarios. With High management, all populations increase to attain maximum carrying capacity. However, growth rates for individual populations are not substantially greater in the High scenario than in the Manger’s or Medium scenarios. This is most likely the consequence of reaching the upper limit to growth set by carrying capacity in the simulated populations. Thus, effects of the High scenario in these instances are not necessarily indicative that implementing greater or more effective management is unlikely to significantly increase populations. Specifically, if carrying capacity estimates are overly conservative, and the high densities of RCWs that occur in very high quality habitat suggest they are, then greater growth than our simulations project and larger differences between management scenarios are possible. Apart from the Bienville National Forest X population, which is in the high resilience class, the five populations that are in the very high resilience category across all management scenarios are the only ones that have the carrying capacities and potential to support very high resilience populations. The ability to support more such populations does not exist currently or within the simulated future 25-year period because of the size of forest tracts with agencies and landowners engaged in RCW conservation. The North Carolina Sandhills population, as previously described, is unique among these largest populations with very high resilience due to the significant contribution of private landowners enrolled in the RCW Safe Harbor program. RCWs supported by these private landowners establish demographic connectivity across larger population segments primarily at Fort Bragg to the northeast and, to the southwest, RCWs at Camp Mackall and Sandhills Gamelands.

Table 31. Population resilience summary for the “very high” category for the High Management scenario. Populations are sorted by rank based on descending λ.

High Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	EGCP	1312	Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest	858	1312	1.017	Very High
1	SH	893	North Carolina Sandhills	781	893	1.005	Very High
1	SACP	622	Fort Stewart	482	622	1.010	Very High
1	EGCP	550	Eglin Air Force Base	504	550	1.004	Very High
1	MACP	540	Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA	496	540	1.003	Very High

Resilience: High

Of the nine populations with high resilience (Table 32), there are seven with increasing growth rates, two that are stable, and none with declining growth. The median size of populations ranges from 254 to 437 active clusters, with the Homochitto National Forest X (254), Savannah River X (259), and Sam Houston National Forest X (256) populations increasing just enough to transition into the high resilience category (250 – 499 active clusters). The Bienville National Forest X, Savannah River X, and Fort Polk-Vernon Unit Kisatchie National Forest populations increase from their initial size, but do not reach carrying capacity. All other populations reach carrying capacities that limit them to the high resilience category. Three populations in the High management scenario high resilience class do not occur as high resilience populations in the Manager’s and Medium scenarios (Appendix 6). The Blackwater River State Forest E-Conecuh National Forest A and B and Bienville National Forest X populations are each established by a demographic merger resulting from sufficient growth of smaller separate populations that does not occur in other management scenarios. The Savannah River X population, with moderate resilience in the Manager’s and Medium scenarios, upon demographically merging with smaller populations increases to attain the high resilience category. The Blackwater River State Forest E population did not exhibit sufficient growth in the Manager’s and Medium scenarios to demographically merge with the Conecuh National Forest A population. This merger in the High scenario established the Blackwater River State Forest E-Conecuh National Forest A and B population in the high resilience category (Appendix 6).

Table 32. Population resilience summary for the "high" category for the High Management scenario. Populations are sorted by rank based on descending λ.

High Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
2	UEGCP	500	Bienville National Forest X	343	437	1.039	High
2	SACP	315	Savannah River X	116	259	1.039	High
1	SACP	300	Osceola National Forest	152	300	1.028	High
1	WGCP	429	Fort Polk-Vernon Unit Kisatchie National Forest	223	392	1.023	High
1	SH	422	Carolina Sandhills NWR-Sandhills State Forest-Cheraw State Park	248	422	1.021	High
1	EGCP	254	Homochitto National Forest	151	254	1.021	High
2	EGCP	417	Blackwater River State Forest E-Conecuh National Forest A and B	323	417	1.021	High
1	SH	410	Fort Benning	386	410	1.002	High
2	UWGCP	256	Sam Houston National Forest X	116	256	1.000	High

Resilience: Moderate

Of the 17 populations with moderate resilience, 11 are increasing and six are stable (Table 33). Ten populations within the moderately resilient class reach a population size that represents 95% or more of carrying capacity. Median population sizes range from 100 to 228 across this broad resilience size-class (100 – 249 active clusters). Six populations (Angelina National Forest X, Brosnan Forest, Winn District Kisatchie National Forest X, DeSoto District DeSoto National Forest A, DeSoto District DeSoto National Forest B and Catahoula X Kisatchie National Forest) are in the low resilience category in all other management scenarios, but increase sufficiently under High management to become moderately resilient populations (Appendix 6). Only one population (Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge) has sufficient carrying capacity to potentially transition into the high resilience class.

Table 33. Population resilience summary for the “moderate” category for the High Management scenario. Populations are sorted by rank based on descending λ. Populations with yellow highlight are at or near carrying capacity.

High Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
2	EGCP	145	DeSoto District DeSoto National Forest A	47	128	1.041	Moderate
1	FP	200	Big Cypress National Preserve A	83	189	1.033	Moderate
2	EGCP	155	Chickasawhay District DeSoto National Forest	69	155	1.033	Moderate
1	WGCP	255	Kisatchie District Kisatchie National Forest A,B,C-Peason Ridge	159	228	1.032	Moderate
1	EGCP	133	DeSoto District DeSoto National Forest B	53	110	1.030	Moderate
1	MACP	138	Croatan National Forest	69	138	1.028	Moderate
1	UEGCP	225	Oakmulgee District A Talladega National Forest	114	225	1.028	Moderate
2	WGCP	155	Winn District Kisatchie National Forest X	88	135	1.024	Moderate
1	WGCP	125	Angelina National Forest X	64	117	1.023	Moderate
1	OM	140	Ouachita National Forest X	101	140	1.023	Moderate
2	WGCP	216	Catahoula X Kisatchie National Forest	78	129	1.023	Moderate
1	MACP	144	Marine Corps Base Camp Lejeune B	89	144	1.019	Moderate
1	P	160	Piedmont NWR-Oconee National Forest-Hithchiti Experimental	83	129	1.018	Moderate
2	FP	120	Withlacoochee State Forest Citrus	82	120	1.015	Moderate
1	WGCP	180	Evangeline Unit Kisatchie National Forest-Alexander State Forest	152	180	1.007	Moderate
1	SACP	100	Brosnan Forest	86	100	1.006	Moderate
1	EGCP	110	Georgia Safe Harbor	97	110	1.005	Moderate

Resilience: Low

The low resilience class consists of 32 populations (Table 34), of which 18 are increasing and 14 are stable. The number and composition of populations in the low resilience class are similar to those in the low resilience class in the Manager’s and Medium scenarios (Figure 27), although these populations generally have equal or greater growth rates in the High scenario (Appendix 6). The lack of transitions out of the low resilience category is not because the simulated management fails to increase populations sufficiently, but rather because carrying capacity limits all 32 populations to the low resilience size-class (30 – 99 active clusters). Thirty populations in fact increase to carrying capacity under High management, and one population (Ocala National Forest C) grows to a median population size that is 96% of its capacity. Fort Gordon is the only population that does not attain carrying capacity in 25 years, but it would reach capacity soon afterwards assuming its average annual growth of 1.053 continues. Management at the more comprehensive and intensive levels represented by the High scenario substantially improves the performance of these populations with inherently low resilience.

Table 34. Population resilience summary for the “low” category for the High management scenario. Populations are sorted by rank based on descending λ.

High Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	WGCP	47	Catahoula A Kisatchie National Forest-Winn Kisatchie National Forest	12	47	1.056	Low
1	SH	96	Fort Gordon	24	87	1.053	Low
1	CRV	75	Shoal Creek District-Talladega National Forest	23	75	1.048	Low
1	OM	45	McCurtain County Wilderness Area	15	45	1.045	Low
1	FP	53	Bull Creek-Triple N WMA	18	53	1.044	Low
1	CRV	39	Talladega	14	39	1.042	Low
1	SACP	34	Okefenokee NWR D	13	34	1.039	Low
1	FP	50	Corbett WMA	30	50	1.035	Low
1	FP	97	Ocala National Forest C	40	93	1.034	Low
1	WGCP	35	Angelina National Forest A	13	35	1.032	Low
1	SACP	30	Webb Wildlife Center	14	30	1.031	Low
1	FP	71	Avon Park Air Force Range	35	71	1.029	Low
1	FP	40	Ocala National Forest B	20	40	1.028	Low
1	UWGCP	60	Sabine National Forest A	32	60	1.025	Low
1	FP	30	Dupuis Wildlife and Environmental Area	15	30	1.025	Low
1	MACP	61	Marine Corps Base Camp Lejeune A	33	61	1.025	Low
1	UWGCP	44	Davy Crockett National Forest B	25	44	1.023	Low
1	SH	70	Fort Jackson	41	70	1.022	Low
1	FP	93	Ocala National Forest A	58	93	1.019	Low
1	EGCP	45	Silver Lake WMA	31	45	1.015	Low
1	FP	65	Three Lakes WMA	45	65	1.015	Low
1	EGCP	45	Jones Ecological Research Center	32	45	1.014	Low
1	SACP	40	Camp Blanding	31	40	1.010	Low
1	UWGCP	75	Davy Crockett National Forest A	59	75	1.010	Low
1	SH	39	Manchester Poinsett	32	39	1.008	Low
1	FP	46	Withlacoochee State Forest Croom	39	46	1.007	Low
2	UEGCP	49	Sam D. Hamilton Noxubee NWR X	41	49	1.006	Low
1	FP	52	Babcock Webb WMA	45	52	1.006	Low
1	UWGCP	40	Sam Houston National Forest F	35	40	1.005	Low
1	MACP	40	Holly Shelter Game Land	36	40	1.004	Low
2	UWGCP	65	Sabine National Forest X	59	65	1.003	Low
1	UWGCP	36	Felsenthal-TNC	35	36	1.001	Low

Resilience: Very Low

Of the 18 populations with very low resilience (Table 35), five increase and 13 remain stable under High management. All of these populations attain carrying capacity under High management, but none have the capacity to transition to a higher resilience category. Populations in this inherently very low resilience class are the most vulnerable to extirpation, but effects of management simulated in the High scenario sustain and in a few cases increase these populations.

Table 35. Population resilience summary for the "very low" category for the High management scenario. Populations are sorted by rank based on descending λ.

High Future Management Scenario							
Code	Ecoregion	Capacity	Population	Initial Size	Median Future Size	λ	Baseline Resilience Class
1	EGCP	19	St. Marks NWR B	6	19	1.047	Very Low
1	SACP	29	Okefenokee NWR B	15	29	1.027	Very Low
1	FP	23	Babcock Ranch Preserve	12	23	1.026	Very Low
1	FP	23	St. Sebastian River Preserve State Park	13	23	1.023	Very Low
1	FP	10	Platt Branch Wildlife and Environmental Area	6	10	1.021	Very Low
1	UWGCP	20	Warren Prairie Natural Area	13	20	1.017	Very Low
1	MACP	21	Piney Grove	14	21	1.016	Very Low
1	FP	13	TNC Disney Wilderness Preserve	9	13	1.015	Very Low
1	MACP	20	Yawkey Wildlife Center	14	20	1.014	Very Low
1	GCPM	27	Big Branch Marsh NWR	20	27	1.012	Very Low
1	UWGCP	20	Sam Houston National Forest D	15	20	1.012	Very Low
1	SACP	14	Okefenokee NWR A	11	14	1.010	Very Low
1	MACP	15	Lewis Ocean Bay Heritage Preserve	12	15	1.009	Very Low
1	WGCP	26	Crowell Lumber	21	26	1.009	Very Low
1	MACP	24	Military Ocean Terminal Supply Point	20	24	1.007	Very Low
2	FP	25	Picayune Strand State Forest X	23	25	1.005	Very Low
1	SACP	9	Okefenokee NWR C	9	9	1.000	Very Low
1	MACP	8	Longleaf Heritage Preserve - Lynchburg Savanna Heritage Preserve	8	8	1.000	Very Low

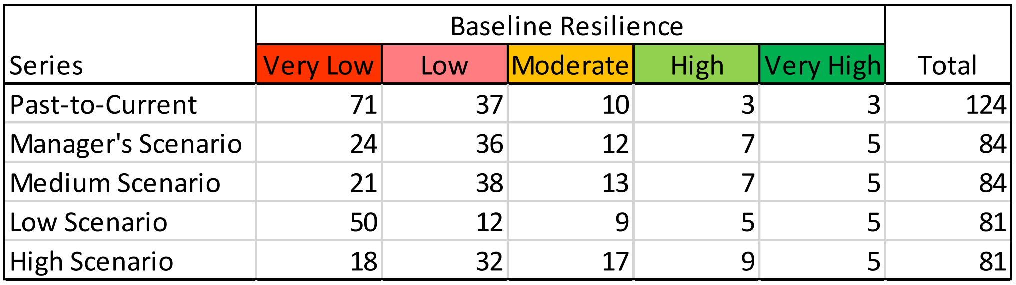
Resilience Summary

The number of existing populations at 25 years varied slightly among the management scenarios, mostly because of differences in the number of initial populations that demographically merged during simulations to establish new and larger populations (Table 36). Results of the Manager's Expectation and Medium scenarios were most similar, while the Low and High scenarios represented more extreme future resilience conditions (Figure 27). These simulations, particularly for the Low and High scenarios, illustrate the extent to which the RCW is a conservation reliant species that depends on appropriate management to sustain its populations. They also show how appropriate management can sustain small populations with low or very low resilience.

There were consistently five populations in the very high resilience class (Apalachicola National Forest-St. Marks NWR-Tate's Hell State Forest, Eglin Air Force Base, Francis Marion National Forest-Bonneau Ferry WMA-Santee Coastal Reserve WMA, Fort Stewart, and North Carolina Sandhills) in all of the future management scenarios (Appendix 6).   Only one other population (Bienville National Forest X) had sufficient carrying capacity to potentially attain very high resilience, but only during the High management scenario upon the growth and merger of smaller Bienville National Forest demographic populations.

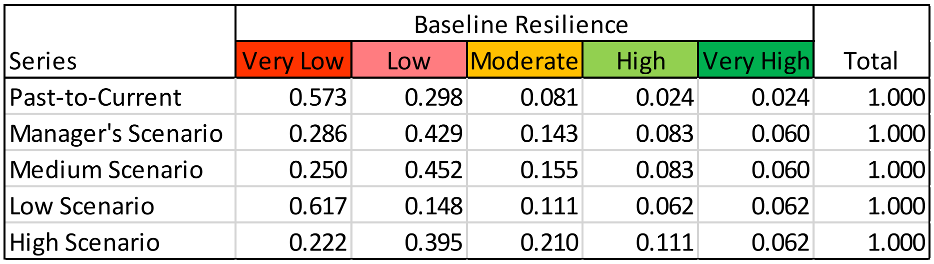
Table 36. Resilience summary based on current condition and population simulations under four future management scenarios. Number of populations for Past-to-Current condition includes all populations with current condition data, including those whose future was not simulated because of insufficient data, and represents their resilience based on population behavior over the past twenty years. The number of existing populations at 25 years is not equal among management scenarios because of the variable number of initial populations that demographically merge to establish new populations during the simulations.

a. Number of current and future simulated populations by resilience class.



	Baseline Resilience					
Series	Very Low	Low	Moderate	High	Very High	Total
Past-to-Current	71	37	10	3	3	124
Manager's Scenario	24	36	12	7	5	84
Medium Scenario	21	38	13	7	5	84
Low Scenario	50	12	9	5	5	81
High Scenario	18	32	17	9	5	81

b. Proportion of current and future simulated populations by resilience class.



	Baseline Resilience					
Series	Very Low	Low	Moderate	High	Very High	Total
Past-to-Current	0.573	0.298	0.081	0.024	0.024	1.000
Manager's Scenario	0.286	0.429	0.143	0.083	0.060	1.000
Medium Scenario	0.250	0.452	0.155	0.083	0.060	1.000
Low Scenario	0.617	0.148	0.111	0.062	0.062	1.000
High Scenario	0.222	0.395	0.210	0.111	0.062	1.000

Overall, the Low management scenario projected very little improvement in resilience compared to current conditions, with an increase in the proportion of populations in the moderate to very high resilience categories from 13% currently (16 of 124 current populations) to 23% (19 of 81 simulated populations) over 25 years. This contrasts with projected increases to 29% (24)under the Manager's Expectation, 30% (25) with Medium management, and 38% (31) with High management. Most small populations are projected to be in serious risk of extirpation under Low management. In the Low management scenario 58 populations are projected to have negative population growth rates, compared to only 11 and two in the Manager's Expectation and Medium and management scenarios respectively. Most populations projected to have negative growth rates are in the very low resilience category: 48/58 Low, 10/11 Manager's Expectation, 2/2 Medium. However, 10/12 populations in the low resiliency category also are projected to have negative growth rates under Low management, compared to only one in the Manager's Expectation and Medium scenarios combined. Thus, under Low management, the number of populations with very low resilience was projected to increase compared to current conditions due to transitions of some populations from low to very low resilience. The opposite occurred in all the other scenarios, that is, the number of populations with very low resilience was project to decrease due to transition of numerous population with very low resilience currently to the low resilience category over 25 years (Figure 27, Table 36, Appendix 6). In contrast, High management was projected to reduce the number of populations with very low resilience the most, as well as increasing the number of populations with moderate to very high resilience the most. No populations were projected to have negative growth rates under High management. Thus, effects of management simulated in the High scenario sustain and in a few cases increase even the populations most vulnerable to extirpation, represented by the very low resilience class.

These results illustrate the dependence of RCW population resilience on management specifically designed for this species (i.e., recruitment clusters, cavity management, translocation, priority habitat restoration). Management that employs these techniques the most (i.e., the High management scenario) is projected to produce the most favorable resilience. The High scenario may represent the limit to what can be accomplished by appropriate management, enabling most populations to increase to carrying capacity and capability of the land base. The scenario in which management techniques designed for RCWs are employed the least (i.e., the Low management scenario) produces the least favorable resilience, projecting a future in which all but the largest RCW populations have declining growth rates and face eventual extirpation. In reality with poor management, even the largest populations that continue to rely on artificial cavities and other management would be expected to decline because the Low scenario model could not effectively remove all positive past management effects to simulate the future degradation of cavities and habitat. The historic population declines that caused the RCW to become endangered illustrate what will happen to the species without the effective ecosystem management that exists today. However, the results of the Low management simulations indicate that ecosystem management alone is not sufficient. Without adequate species-level management in addition to ecosystem management alone, very little increase in the number of moderately to very highly resilient populations can be expected, and small populations of low or very low resilience are unlikely to persist. In contrast, should management continue even at current levels as represented by the Medium Management scenario, further increases in the number of moderate to very high resilient populations can be expected, and small populations can be preserved, and again, with more intense management as represented by High management, only the carrying capacity of available habitat limits the future population size of the RCW.

Future Species Representation and Redundancy

Under all the management scenarios, there are five populations in the very high resilience category, occurring in the East Gulf Coastal Plain (EGCP – 2), Sandhills (SH – 1), Mid- Atlantic Coastal Plain (MACP – 1), and South-Atlantic Coastal Plain (1 – SACP) (Figure 27, Table 37, Appendix 6). In the Manager’s Expectation and Medium Management scenarios, there are seven populations in the high resilience category, located in EGCP, SACP, SH, Upper West Gulf

Coastal Plain (UWGCP) and West Gulf Coastal Plain (WGCP). Thus, six ecoregions contain populations of high or very high resilience. Two of these populations with high resilience are projected to have only moderate resilience in the Low Management scenario (Sam Houston National Forest X and Homochitto National Forest, Appendix 6), and thus only five ecoregions contain populations of high or very high resilience. Under High management, nine populations are projected to have high resilience, such that an additional, seventh ecoregion (Upper East Gulf Coastal Plain) contains a population of high to very high resilience. Compared to current conditions, a greater number of high and very high resilience populations are projected to be more widely distributed among ecoregions and to include the western geographic range under Medium and High management in the future. Over the wide geographic range of this species, the occurrence of high and very high resilience populations is most concentrated in the EGCP and SH.

Six ecoregions (Cumberland Ridge and Valley-CRV, Florida Peninsula-FP, Gulf Coast Prairie Marshes-GCPM, Mississippi River Alluvial Plain-MRAP, Ouachita Mountains-OM, and Piedmont-P) currently do not have any populations in the moderate to very high resilience classes (Table 10). The only population in the Mississippi River Alluvial Plain was not simulated for its future condition. Only two ecoregions (CRV, GCPM) have no future simulated populations of moderate to very high resilience in the Manager's Expectation, Medium and High Management scenarios. In the Low Management scenario, four ecoregions with six simulated populations (CRV, GCPM, OM, and P) are restricted to very low and low resilience classes, without any of moderate to very high resilience at 25 years. Compared to current conditions, there is potential to make significant gains in representation and redundancy over the next 25 years, but only with future management represented by the Manager's Expectation, Medium, and High scenarios.

Table 37**.** Future redundancy and representation summary for RCW ecoregions by number of simulated populations and resilience category under future management scenarios. The All category in each scenario is all simulated populations plus other currently delineated demographic populations that were not simulated because of either inadequate data or small population size (i.e., < 6 active clusters. Ecoregions: CRV (Cumberland Ridge Valley); EGCP (East Gulf Coastal Plain); FP (Florida Peninsula); GCPM (Gulf Coast Prairie Marshes); MACP (Mid-Atlantic Coastal Plain); MRAP (Mississippi River Alluvial Plain); OM (Ouachita Mountains); P (Piedmont); SACP (South Atlantic Coastal Plain); SH (Sandhills); UEGP (Upper East Gulf Coastal Plain); UWGCP (Upper West Gulf Coastal Plain); and WGCP (West Gulf Coastal Plain).

A. Manager's Expectation Scenario

Manager's Scenario							
	Baseline Resilience Size-Class Category						
Ecoregion	Very Low	Low	Moderate	High	Very High	Total	All
EGCP	1	5	2	2	2	12	14
SACP	5	2	1	1	1	10	10
SH	0	3	0	2	1	6	6
MACP	5	2	2	0	1	10	23
UWGCP	2	6	0	1	0	9	15
WGCP	2	4	2	1	0	9	9
FP	6	9	2	0	0	17	21
UEGP	1	2	2	0	0	5	6
OM	1	0	1	0	0	2	2
CRV	0	2	0	0	0	2	2
P	0	1	0	0	0	1	2
GCPM	1	0	0	0	0	1	1
MRAP	0	0	0	0	0	0	1
Total	24	36	12	7	5	84	112

B. Low Scenario

Low Scenario							
	Baseline Resilience Size-Class Category						
Ecoregion	Very Low	Low	Moderate	High	Very High	Total	All
EGCP	4	3	2	1	2	12	14
SACP	6	1	0	1	1	9	9
SH	3	0	0	2	1	6	6
MACP	7	1	1	0	1	10	23
UWGCP	6	1	1	0	0	8	14
WGCP	3	3	1	1	0	8	8
FP	14	1	2	0	0	17	21
UEGP	3	0	2	0	0	5	6
OM	1	1	0	0	0	2	2
CRV	2	0	0	0	0	2	2
P	0	1	0	0	0	1	2
GCPM	1	0	0	0	0	1	1
MRAP	0	0	0	0	0	0	1
Total	50	12	9	5	5	81	109

Table 37. Continued

C. Medium Scenario

Medium Scenario							
	Baseline Resilience Size-Class Category						
Ecoregion	Very Low	Low	Moderate	High	Very High	Total	All
EGCP	1	5	2	2	2	12	14
SACP	4	3	1	1	1	10	10
SH	0	3	0	2	1	6	6
MACP	5	2	2	0	1	10	23
UWGCP	2	6	0	1	0	9	15
WGCP	1	5	2	1	0	9	9
FP	6	9	2	0	0	17	21
UEGP	0	3	2	0	0	5	6
OM	1	0	1	0	0	2	2
CRV	0	2	0	0	0	2	2
P	0	0	1	0	0	1	2
GCPM	1	0	0	0	0	1	1
MRAP	0	0	0	0	0	0	1
Total	21	38	13	7	5	84	112

D. High Scenario

High Scenario							
	Baseline Resilience Size-Class Category						
Ecoregion	Very Low	Low	Moderate	High	Very High	Total	All
EGCP	1	2	4	2	2	11	13
SACP	3	3	1	2	1	10	10
SH	0	3	0	2	1	6	6
MACP	5	2	2	0	1	10	23
UWGCP	2	6	0	1	0	9	15
WGCP	1	2	5	1	0	9	9
FP	5	10	2	0	0	17	21
UEGP	0	1	1	1	0	3	4
OM	0	1	1	0	0	2	2
CRV	0	2	0	0	0	2	2
P	0	0	1	0	0	1	2
GCPM	1	0	0	0	0	1	1
MRAP	0	0	0	0	0	0	1
Total	18	32	17	9	5	81	109

LITERATURE CITED

Affeltranger, C. 1971. The red heart disease of southern pines. Pp. 96-99 *in* R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bureau of Sport Fishing and Wildlife and Tall Timbers Research Station, Tallahassee, FL.

Aldredge, R. A., E. N. Angell, L. Gilson, G. R. Schrott, and R. Bowman. 2016. Translocations reverse high hatching failure in a small, isolated population of red-cockaded woodpeckers. Presentation to Red-cockaded Woodpecker Southern Range Translocation Cooperative. U.S. Fish and Wildlife Service RCW Recovery Coordinator file.

Allen, D. H. 1991. Constructing artificial red-cockaded woodpecker cavities. USDA Forest Service General Technical Report SE-73.

American Ornithologists' Union. 1947. Twenty-second supplement to the American Ornithologists' Union check-list of North American birds. The Auk 64:445-452.

American Ornithologists' Union. 1982. Thirty-fourth supplement to the American Ornithologists' Union check-list of North American birds. The Auk 99 (3) Supplement.

Bailey, A. D., R. Mickler, and C. Frost. 2007. Presettlement fire regime and vegetation mapping in southeastern coastal plain forest ecosystems. Pp. 275-286 *in* B. W. Butler and W. Cook, compilers. The fire environment: innovations, management, and policy. Conference proceedings, 26-30 March, Destin, FL. USDA Forest Service, RMRS-P-46CD. Fort Collins, CO.

Bailey, R. G. 1983. Delineation of ecosystem regions. Environmental Management 7:365-373.

Bailey, R. G., M. E. Jansen, M. T. Cleland, and P. S. Bourgeron. 1994. Design and use of ecological mapping units. Pp. 95-106 in M. E. Jensen and P. S. Bourgeron, eds. Ecosystem management: principles and applications. Volume 1. USDA Forest Service General Technical Report PNWGTR-318.

Bailey, R. G. 2016. Bailey's ecoregions and subregions of the United States, Puerto Rico, and the U.S. Virgin Islands GIS. USDA Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2016-003.

Bainbridge, B., K. A. Baum, D. Saenz, and C. K. Adams. 2011. Red-cockaded woodpecker cavity-tree damage by Hurricane Rita: an evaluation of contributing factors. Southeastern Naturalist 10:11-24.

Baker, W. W. 1971a. Observation of the food habits of the red-cockaded woodpecker. Pp. 100-

107 *in* R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bureau of Sport Fishing and Wildlife and Tall Timbers Research Station, Tallahassee, FL.

Baker, W. W. 1971b. Progress report on life history studies of the red-cockaded woodpecker at Tall Timbers Research Station. Pp. 44-59 *in* R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bureau of Sport Fisheries and Wildlife and Tall Timbers Research Station, Tallahassee, FL.

Baker, W. W. 1981. The distribution, status, and future of the red-cockaded woodpecker in Georgia. Pp. 82-87 in R. R. Odom and J. W. Guthrie, eds. Proceedings of the nongame and endangered wildlife symposium. Georgia Department of Natural Resources, Game and Fish Division, Technical Bulletin WL5.

Beal, F. E. L., W. L. McAtee, and E. R. Kalmbach. 1941. Red-cockaded woodpecker. Pages 33-35 *in* Common birds of southeastern United States in relation to agriculture. U.S. Fish and Wildlife Service Conservation Bulletin 15.

Beaty, T. A. , A. E. Bivings, T. G. Reid, T. L. Myers, S. D. Parris, R. Costa, T. J. Hayden, and T. E. Ayers. 2004. Success of the Army's 1996 red-cockaded woodpecker management guidelines. Pages 109-115 *in* R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

Beckett, T. A., III. 1971. A summary of red-cockaded woodpecker observations in South Carolina. Pages 87-95 *in* R. L. Thompson, editor. The ecology and management of the red-cockaded woodpecker. Bureau of Sport Fisheries and Wildlife, U.S. Department of the Interior, and Tall Timbers Research Station, Tallahassee, Florida, USA.

Beever, J. W. III, and K. A. Dryden. 1992. Red-cockaded woodpeckers and hydric slash pine flatwoods. Transactions of the 57th North American Wildlife and Natural Resources Conference 57:693-700.

Beyer, D. E., R. Costa, R. G. Hooper, and C. A. Hess. 1996. Habitat quality and reproduction of red-cockaded woodpecker groups in Florida. Journal of Wildlife Management 60:826-835.

Bowman R., and C. Huh. 1995. Tree characteristics, resin flow, and heartwood rot in pines (Pinus palustris, P. elliottii), with respect to red-cockaded woodpecker cavity excavation, in two hydrologically-distinct Florida flatwood communities. Pp. 415-426 in D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, TX.

Bowman, R., D. L. Leonard, L. M. Richman, and L. K. Backus. 1997. Demography of the red-cockaded woodpecker at the Avon Park Air Force Range. Report Number F08602-96-D0015. Archbold Biological Station, Lake Placid, FL.

Bowman, R., D. L. Leonard, D. Swan, and D. Schwalm. 2004. Demography and population trends of a small red-cockaded woodpecker population in South-Central Florida. Page 187-197 *in* R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

Bradshaw, D. S. 1995. Habitat use by a relict population of red-cockaded woodpeckers in southeastern Virginia. Pp. 482-488 in D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, TX.

Bragg, D. C. 2002. Reference conditions for old-growth pine forests in the Upper West Gulf Coastal Plain. Journal of the Torrey Botanical Society 129:261-288.

Bragg, D. C., R. O'Neil, W. Holimon, J. Fox, G. Thornton, and R. Mangham. 2014. Moro Big Pine: conservation in the pine flatwoods of Arkansas. Journal of Forestry 112:446-456.

Bruggeman, D. J. 2013. Evaluation of encroachment partnering parcels on the Fort Benning landscape using landscape equivalency analysis and pattern oriented modeling for red-cockaded woodpeckers. Report to The Nature Conservancy. Ecological Services and Markets, Inc., Asheville, NC.

Bruggeman, D. J. and M. Jones 2014. Development of adaptive management tools to guide habitat allocations for at-risk species. Final Report, SERDP Project RC-1656. Strategic Environmental Research and Development Program, Arlington, Virginia, USA.

Brust, K., R. Speckman, J. H. Carter, III, and A. Esposito. 2004. Endangered species management plan for the Palmetto-Peartree Preserve, Tyrell County, North Carolina. The Conservation Fund, Chapel Hill, NC.

Bryant, D. and J. Boykin. 2007. Fuels management on the National Forests in Mississippi after Hurricane Katrina. Pages 287-292 *in* B. W. Butler and W. Cook, compilers. The fire environment - innovations, management, and policy. Conference proceedings RMRS-P-46CD. USDA Forest Service, Rocky Mountain Research Station.

Butler, M. J. 2001. Red-cockaded woodpecker foraging habitat requirements on industrial forests in southern Arkansas and northern Louisiana. Thesis, University of Arkansas at Monticello, Monticello, Arkansas, USA.

Carr, S. C., K. M. Robertson, W. J. Platt, and R. K. Peet. 2009. A model of geographical, environmental and regional variation in vegetation composition of pyrogenic grasslands of Florida. Journal of Biogeography 36:1600-1612.

Carrie, N. R., K. R. Moore, S. A. Stephens, and E. L. Keith. 1998. Influence of cavity availability on red-cockaded woodpecker group size. Wilson Bulletin 110:93-99.

Carter, J. H., III. 1971. Birds of the central Sandhills of North Carolina: red-cockaded woodpecker. Chat 35:98.

Carter, J. H., III, R. T. Stamps, and P. D. Doerr. 1983. Status of the red-cockaded woodpecker in the North Carolina Sandhills. Pages 24-29 *in* D. A. Wood, editor. Red-cockaded woodpecker symposium II proceedings. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.

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

Carter, J. H. III, and K. Brust. 2004. The red-cockaded woodpecker in the northeastern Coastal Plain of North Carolina. Pages 268-277 *in* R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

Caswell, H. 1989. Matrix population models. Sinauer Associates, Sunderland, MA.

Chesser, R. T., K. J. Burns, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen, Jr., D. F. Stotz, B. M. Winger, and K. Winker. 2018. Fifty-ninth supplement to the American Ornithological Society's Checklist of North American Birds. The Auk 135:798-813.

Christensen, N. L. 2000. Vegetation of the southeastern Coastal Plain. Pp. 397-448 in Barbour, M. G., and W. D. Billings, eds. North American terrestrial vegetation. Second edition. Cambridge University Press, Cambridge, UK.

Clark, A., III. 1992. Heartwood formation in loblolly and longleaf pines for red-cockaded woodpecker nesting cavities. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 46:79-87.

Clark, A., III. 1993. Characteristics of timber stands containing sufficient heartwood for cavity excavation by red-cockaded woodpecker clans. Pages 621-626 *in* J. C. Brissette, editor. Proceedings of the seventh biennial southern silvicultural conference. U.S. Forest Service

General Technical Report SO-93.

Cleland, D. T., P. E. Avers, W. H. McNab, M. E. Jensen, R. G. Bailey, T. King, and W. E. Russell. 1997. National hierarchical framework of ecological units. Pages 181-200 *in* M. S. Boyce and A. Haney, editors. Ecosystem management applications for sustainable forest and wildlife resources. Yale University Press, New Haven, CT.

Cleland, D. T., J. A. Freeouf, J. E. Keys, Jr., G. J. Nowacki, C. Carpenter, and W. H. McNab. 2007. Ecological subregions: sections and subsections of the conterminous United States. A. M. Sloan, cartographer. USDA Forest Service,General Technical Report WO-76. Washington, DC.

Clements, F. E., and V. Shelford. 1939. Bioecology. John Wiley, New York, NY.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, D. Roberson T. A. Fredericks, B. L. Sullivan, and C. L. Wood. 2017. The eBird/Clements checklist of birds of the world: v2017. The Cornell Lab of Ornithology. Ithaca, NY.

Collins, C. S. 1998. The influence of hardwood midstory and pine species on pine bole arthropod communities in eastern Texas. M.Sc. thesis, Stephen F. Austin State University, Nacogdoches, TX.

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

Conner, R. N., and B. A. Locke. 1982. Fungi and red-cockaded woodpecker cavity trees. Wilson Bulletin 94:64-70.

Conner, R. N., and B. A. Locke. 1983. Artificial inoculation of red heart fungus into loblolly pines. Pages 81-82 *in* D. A. Wood, editor. Red-cockaded woodpecker symposium II proceedings. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.

Conner, R. N., and K. A. O'Halloran. 1987. Cavity-tree selection by red-cockaded woodpeckers as related to growth dynamics of southern pines. Wilson Bulletin 99:398-412.

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

Conner, R. N., and D. C. Rudolph. 1991. Effects of midstory reduction and thinning in red-cockaded woodpecker cavity tree clusters. Wildlife Society Bulletin 19:63-66.

Conner, R. N., D. C. Rudolph, D. L. Kulhavy, and A. E. Snow. 1991a. Causes of mortality of red-cockaded woodpecker cavity trees. Journal of Wildlife Management 55:531-537.

Conner, R. N., A. E. Snow, and K. A. O'Halloran. 1991b. Red-cockaded woodpecker use of seedtree/shelterwood cuts in eastern Texas. Wildlife Society Bulletin 19:67-73.

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. Journal of Wildlife Management 58:728-734.

Conner, R. N., D. C. Rudolph, and L. H. Bonner. 1995. Red-cockaded woodpecker population trends and management on Texas national forests. Journal of Field Ornithology 66:140-151.

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 in Forestry, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Conner, R. N., and D. C. Rudolph. 1995b. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. Wilson Bulletin 107:81-92.

Conner, R. N., and D. C. Rudolph. 1995c. Wind damage to red-cockaded woodpecker cavity trees on eastern Texas national forests. Pp. 183-190 in D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, TX.

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 Bulletin 108:697-711.

Conner, R. N., D. C. Rudolph, D. Saenz, and R. N. Coulson. 1997a. The red-cockaded woodpecker’s role in the southern pine ecosystem, population trends and relationships with southern pine beetles. Texas Journal of Science 49 Supplement:139-154.

Conner, R. N., D. C. Rudolph, D. Saenz, and R. R. Schaefer. 1997b. Species using red-cockaded woodpecker cavities in eastern Texas. Bulletin of the Texas Ornithological Society 30:11-16.

Conner, R. N., D. C. Rudolph, R. R. Schaefer, and D. Saenz. 1997c. Long-distance dispersal of redcockaded woodpeckers in Texas. Wilson Bulletin 109:157-160.

Conner, R. N., D. Saenz, D. C. Rudolph, W. G. Ross, and D. L. Kulhavy. 1998a. Red-cockaded woodpecker nest-cavity selection: relationships with cavity age and resin production. Auk 115:447-454.

Conner, R. N., D. Saenz, D. C. Rudolph, and R. N. Coulson. 1998b. Southern pine beetle-induced mortality of pines with natural and artificial red-cockaded woodpecker cavities in Texas. Wilson Bulletin 110:100-109.

Conner, R. N., D. C. Rudolph, R. R. Schaefer, D. Saenz, and C. E. Shackelford. 1999. Relationships among red-cockaded woodpecker group density, nestling provisioning rates, and habitat. Wilson Bulletin 111:494-498.

Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001a. The red-cockaded woodpecker surviving in a fire-maintained ecosystem. University of Texas Press, Austin, Texas, USA.

Conner, R. N., J. R. McCormick, R. R. Schaefer, D. Saenz, and D. C. Rudolph. 2001b. A red-cockaded woodpecker group with two simultaneous nest trees. Wilson Bulletin 113:101-104.

Conner, R. N., D. Saenz, R. R. Schaefer, J. R. McCormick, D. C. Rudolph, and D. B. Burt. 2005. Rainfall, El Nino, and reproduction of red-cockaded woodpeckers. Southeastern Naturalist 4:347-354.

Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications 5:17-19.

Convery, K. M. 2002. Assessing habitat quality for the endangered red-cockaded woodpecker (*Picoides borealis*). Thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Copeyon, C. K. 1990. A technique for constructing cavities for the red-cockaded woodpecker. Wildlife Society Bulletin 18:303-311.

Copeyon, C. K., J. R. Walters, and J. H. Carter, III. 1991. Induction of red-cockaded woodpecker group formation by artificial cavity construction. Journal of Wildlife Management 55:549-556.

Costa, R., and R. Escano. 1989. Red-cockaded woodpecker: status and management in the southern region in 1986. U.S. Forest Service Technical Publication R8-TP12.

Costa, R., and J. L. Walker. 1995. Red-cockaded woodpecker. Pages 86-89 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. National Biological Service, Washington, D.C., USA.

Costa, R. 2001. Red-cockaded woodpecker. Pages 309-321 *in* J.G. Dickson, editor. Wildlife of southern forests: habitat and management. Hancock House, Blaine, Washington, USA.

Costa, R., and R. S. DeLotelle. 2006. Reintroduction of fauna to longleaf pine ecosystems: opportunities and challenges. Pages 335-376 *in* S. Jose, E. J. Jokela, and D. L. Miller, editors. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer Science + Business Media, Inc., New York, USA.

Crosby, G. T. 1971. Home range characteristics of the red-cockaded woodpecker in north-central Florida. Pp. 60-73 in R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bureau of Sport Fishing and Wildlife and Tall Timbers Research Station, Tallahassee, FL.

Crowder, L. B., J. A. Priddy, and J. R. Walters. 1998. Demographic isolation of red-cockaded woodpecker groups: a model analysis. Project Final Report, prepared for U.S. Fish and Wildlife Service.

Daniels, S. J. 1997. Female dispersal and inbreeding in the red-cockaded woodpecker. M.Sc. thesis, Virginia Polytechnic Institute and State University, Blacksburg VA.

Daniels, S. J., J. A. Priddy, and J. R. Walters. 2000. Inbreeding in small populations of red-cockaded woodpeckers: insights from a spatially explicit individual-based model. Pages 129-147 *in* A. G. Young, and G. M. Clarke, editors. Genetics, demography and viability of fragmented populations. Cambridge University Press, London, UK.

Daniels, S. J., and J. R. Walters. 2000a. Inbreeding depression and its effects on the natal dispersal of red-cockaded woodpeckers. Condor 102:482-491.

Daniels, S. J., and J. R. Walters. 2000b. Between-year breeding dispersal in red-cockaded woodpeckers: multiple causes and estimated cost. Ecology 81:2473-2484.

Dare County Bombing Range. 2007. Endangered species management plan for the red-cockaded woodpecker (*Picoides borealis*). Seymour Johnson Air Force Base, Goldsboro, NC.

Dawson, W. L., and L. Jones. 1903. The birds of Ohio. Volume 1. Wheaton, Columbus, Ohio.

DeAngelis, D. L., and J. Gross, eds. 1992. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Chapman and Hall, New York.

Delcourt, H. R. and P. A. Delcourt. 1991. Late Quaternary Vegetation History of the Interior Highlands of Missouri, Arkansas, and Oklahoma. Pages - in D. Henderson and L. D. Hedrick, editors. Proc: Restoration of Old Growth Forests of the Interior Highlands of Arkansas and Oklahoma. Winrock International. Morrilton, Ark.

DeLotelle, R. S., J. R. Newman, and R. J. Epting. 1983. Habitat use by red-cockaded woodpeckers in central Florida. Pp. 59-67 in D. A. Wood, ed. Red-cockaded woodpecker symposium II. Florida Game and Fresh Water Fish Commission, Tallahassee, FL.

DeLotelle, R. S., R. J. Epting, and J. R. Newman. 1987. Habitat use and territory characteristics of red-cockaded woodpeckers in central Florida. Wilson Bulletin 99:202-217.

DeLotelle, R. S., and R. J. Epting. 1988. Selection of old trees for cavity excavation by red-cockaded woodpeckers. Wilson Bulletin 16:48-52.

DeLotelle, R. S., and R. J. Epting. 1992. Reproduction of the red-cockaded woodpecker in central Florida. Wilson Bulletin 104:285-294.

DeLotelle, R. S., R. J. Epting, and G. Demuth. 1995. A 12-year study of red-cockaded woodpeckers in central Florida. Pages 259-269 *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 University, Nacogdoches, Texas, USA.

DeLotelle, R. S., D. L. Leonard, and R. J. Epting. 2004. Hatch failure and brood reduction in three central Florida red-cockaded woodpecker populations. Pages 616-623 *in* R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

Dennis, J. V. 1971. Utilization of pine resin by the red-cockaded woodpecker and its effectiveness in protecting roosting and nest sites. Pages 78-86 *in* R. L. Thompson, editor. The ecology and management of the red-cockaded woodpecker. Bureau of Sport Fisheries and Wildlife, U.S. Department of the Interior, and Tall Timbers Research Station, Tallahassee, Florida, USA.

Doerr, P. D., J. R. Walters, and J. H. Carter, III. 1989. Reoccupation of abandoned clusters of cavity trees (colonies) by red-cockaded woodpeckers. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 43:326-336.

Doster, R. H., and D. A. James. 1998. Home range size and foraging habitat of red-cockaded woodpeckers in the Ouachita Mountains of Arkansas. Wilson Bulletin 110:110-117.

Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications 5:3-11.

Ellis, K. N., L. M. Sylvester, and J. C. Trepanier. 2014. Spatiotemporal patterns of extreme hurricanes impacting US coastal cities. Natural Hazards 75: 2733-2749.

Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. Pp. 301 *in* J. R. Krebs and N. B. Davies, eds. Behavioral ecology: an evolutionary approach. Third edition. Blackwell Scientific Publications, Oxford, UK.

Engstrom, R. T., and D. V. Evans. 1990. Hurricane damage to red-cockaded woopecker (*Picoides borealis*) cavity trees. Auk 107:608-609.

Engstrom, R. T., L. A. Brennan, W. L. Neel, R. M. Farrar, S. T. Lindeman, W. K. Moser, and S. M. Hermann. 1996. Silvicultural practices and red-cockaded woodpecker management: a reply to Rudolph and Conner. Wildlife Society Bulletin 24:334-338.

Engstrom, R. T., and F. J. Sanders. 1997. Red-cockaded woodpecker foraging ecology in an old-growth longleaf pine forest. Wilson Bulletin 109:203-217.

Epting, R. T., R. S. DeLotelle, and T. Beaty. 1995. Red-cockaded woodpecker territory and habitat use in Georgia and Florida. Pages 270-276 *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 University, Nacogdoches, Texas, USA.

Ferral, D. P., J. W. Edwards, and A. E. Armstrong. 1997. Long-distance dispersal of red-cockaded woodpeckers. Wilson Bulletin 109:154-157.

Fitch, H. S. 1963. Natural history of the black rat snake (Elaphe o. obsoleta) in Kansas. Copeia 1963:649-658.

Fuchs, J. and J. M. Pons. 2015. A new classification of the Pied Woodpecker assemblage (Dendropicini:Picidae) based on a comprehensive multi-locus phylogeny. Molecular Phylogenetics and Evolution 88:28-37.

Foti, T. L., and S. M. Glenn. 1991. The Ouachita Mountain landscape at the time of settlement. Pp. 49-66 in D. Henderson and L. D. Hedrick, eds. Restoration of old growth forests in the interior highlands of Arkansas and Oklahoma. Winrock International Institute for Agricultural Development, Morrilton, AR.

Frankel, O. H. and M. E. Soule. 1981. Conservation and evolution. Cambridge University Press.

Franklin, I. R. 1980. Evolutionary change in small populations. Pp. 135-139 *in* M. E. Soule and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, MA.

Franklin, I. R., and R. Frankham. 1998. How large must populations be to retain evolutionary potential? Animal Conservation 1:69-70.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pp. 17-44 in S. M. Hermann, ed. The longleaf pine ecosystem: ecology, restoration, and management. Tall Timbers Fire Ecology Conference Proceedings, No. 18. Tall Timbers Research Station, Tallahassee, FL.

Frost, C. C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. Pp. 70-81 in T. L. Pruden and L. A. Brennan, eds. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, No. 20. Tall Timbers Research Station, Tallahassee, FL.

Frost, C. 2006. History and future of the longleaf pine ecosystem. In: Jose, S.; Jokela, E.J.; Miller, D.L., eds. The longleaf ecosystem: ecology, silviculture and restoration. New York: Springer Science: 9–48.

Garabedian, J. E., C. E. Moorman, M. N. Peterson., and J. C. Kilgo. 2014. Systematic review of the influence of foraging habitat on red-cockaded woodpecker reproductive success. Wildlife Biology 20:37-46.

Garabedian, J. E., C. E. Moorman, M. N. Peterson., and J. C. Kilgo. 2017. Use of LiDAR to define habitat thresholds for forest bird conservation. Forest Ecology and Management 399:24-36.

Garabedian, J. E., C. E. Moorman, M. N. Peterson, and J. C. Kilgo. 2018. Evaluating interactions between space-use sharing and defence under increasing density confitions for the group-territorial red-cockaded woodpecker (*Leuconotopicus borealis*). Ibis: early view January 3, 2018.

Gentry, T. G. 1877. *Picus borealis*. Pages 126-128 *in* Life histories of birds of eastern Pennsylvania. Volume 2. J.H. Choate, Salem, Massachusetts, USA.

Gill, F. and D. Donsker. Editors. 2018. International Ornithological Congress world bird list v8.2. doi: 10.14344/IOC.ML.8.2.

Gilliam, F. S., W. J. Platt and R. K. Peet. 2006. Natural disturbances and the physiognomy of pine savannas: a phenomenological model. Applied Vegetation Science 9:83-96.

Grimes, T. L. 1977. Relationship of red-cockaded woodpecker (*Picoides borealis*) productivity to colony area characteristics. M.Sc. thesis, Clemson University, Clemson, SC.

Gowaty, P. A., and M. R. Lennartz. 1985. Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. American Naturalist 126:347-353.

Guan, S. 2014. Post-hurricane fuel dynamics and forest regeneration of coastal pine stands in southeast United States. Thesis. Clemson University, Clemson, SC.

Guldin, J. M., F. R. Thompson, L. L. Richards, and K. C. Harper. 1999. Status and trends of vegetation. Pages 21-70 *in* Ozark-Ouachita highland assessment: terrestrial vegetation and wildlife. General Technical Report SRS-35, USDA Forest Service. Asheville, NC.

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. Conservation Biology 7:289-301.

Haig, S. M., R. Bowman, and T. D. Mullins. 1996. Population structure of red-cockaded woodpeckers in south Florida: RAPDs revisited. Molecular Ecology 5:725-734.

Haig, S. M., J. M. Rhymer, and D. G. Heckel. 1994a. Population differentiation in randomly amplified polymorphic DNA of red-cockaded woodpeckers. Molecular Ecology 3:581-595.

Haig, S. M., J. R. Walters, and J. H. Plissner. 1994b. Genetic evidence for monogamy in the cooperatively breeding red-cockaded woodpecker. Behavioral Ecology and Sociobiology 34:295-303.

Hamrick, D. 1992. Assisting homeless woodpeckers: red-cockaded woodpeckers affected by hurricane Hugo. Birds International 3:18-27.

Hardesty, J. L., K. E. Gault, and F. P. Percival. 1997. Ecological correlates of red-cockaded woodpecker (Picoides borealis) foraging preference, habitat use, and home range size in northwest Florida (Eglin Air Force Base). Final Report Research Work Order 99, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville FL.

Harding, S. R. 1997. The dynamics of cavity excavation and use by the red-cockaded woodpecker (*Picoides borealis*). M.Sc. thesis. Virginia Polytechnic Institute and State

University, Blacksburg VA.

Harding, S. R., and J. R. Walters. 2002. Processes regulating the population dynamics of red-cockaded woodpecker cavities. Journal of Wildlife Management 66:1083-1095

Hanula, J. L., and K. E. Franzreb. 1995. Arthropod prey of nestling red-cockaded woodpeckers in the upper coastal plain of South Carolina. Wilson Bulletin 107:485-495.

Hanula, J. L., and K. E. Franzreb. 1998. Source, distribution, and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. Forest Ecology and Management 102:89-102.

Hanula, J. L., and R. T. Engstrom. 2000. Comparison of red-cockaded woodpecker (*Picoides borealis*) nestling diet in old-growth and old-field longleaf pine (*Pinus palustris*) habitats. American Midland Naturalist 144:370-376.

Hanula, J. L., K. E. Franzreb, and W. D. Pepper. 2000a. Longleaf pine characteristics associated with arthropods available for red-cockaded woodpeckers. Journal of Wildlife Management 64:60-70.

Hanula, J. L., D. Lipscomb, K. E. Franzreb, and S. C. Loeb. 2000b. Diet of nestling red-cockadedwoodpeckers at three locations. Journal of Field Ornithology 71:126-134.

Hardesty, J. L., K. E. Gault, and F. P. Percival. 1997. Ecological correlates of red-cockaded woodpecker (*Picoides borealis*) foraging preference, habitat use, and home range size in northwest Florida (Eglin Air Force Base). Final Report Research Work Order 99, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville FL.

Harlow, R. F., and M. R. Lennartz. 1977. Foods of nestling red-cockaded woodpeckers in coastal South Carolina. Auk 94:376-377.

Harlow, R. F., and A. T. Doyle. 1990. Food habits of southern flying squirrels (*Glaucomys volans*) collected from red-cockaded woodpecker (*Picoides borealis*) colonies in South Carolina. American Midland Naturalist 124:187-191.

Hartl, D. L. 1988. A primer of population genetics. Sinauer Associates, Sunderland MA.

Hausman, L. A. 1928. Red-cockaded woodpecker (*Dryobates borealis*). Page 21 *in* Woodpeckers, nuthatches and creepers of New Jersey. New Jersey Agricultural Experiment Station , New Brunswick, New Jersey, USA.

Hedrick, L. D., G. A. Bukenhofer, W. G. Montague, W. F. Pell, and J. M. Guldin. 2006. Shortleaf pine-bluestem restoration in the Ouachita National Forest. Pages 206-213 *in* J. M.

Kabrick, D. C. Dey and D. Gwaze, editors. Shortleaf pine restoration and ecology in the Ozarks: proceedings of a symposium. USDA Forest Service General Technical Report NRS-P-15. Newton Square, PA.

Hendry, A. P., Kinnison, M. T., Heino, M., Day, T., Smith, T. B., Fitt, G., Bergstromm, C.T., Oakeshott, J., Jorgensen, P.S., Zalucki, M.P., Gilchrist, G., Southerton, S., Sih, A., Strauss, S., Denison, R.F., Carroll, S. P. 2011. Evolutionary principles and their practical application. Evolutionary Applications 4:159–183.

Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. Journal of Wildlife Management 58:479-487.

Hess, C. A., and F. C. James. 1998. Diet of the red-cockaded woodpecker in the Apalachicola National Forest. Journal of Wildlife Management 62:509-517.

Hicks, R. R., Jr., J. E. Coster, and G. N. Mason. 1987. Forest insect hazard rating. Journal of Forestry 85:20-26

Hiers, J. K., J. R. Walters, R. J. Mitchell, J. M. Varner, L. M. Conner, L. A. Blanc, and J. Stowe. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. The Journal of Wildlife Management 78:383-393.

Hines, M., and P. J. Kalisz. 1995. Foraging of red-cockaded woodpeckers (*Picoides borealis*) in Kentucky. Transactions of the Kentucky Academy of Science 56:109-113.

Hodges, J. D., W. W. Elam, and W. F. Watson. 1977. Physical properties of the oleoresin system of four major southern pines. Canadian Journal of Forest Research 7:520-525.

Hodges, J. D., Elam, W. W., Watson, W. F., and Nebeker, T. E. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks.Canadian Entomology 111:889-896.

Hooper, R. G., A. F. Robinson, Jr., and J. A. Jackson. 1980. The red-cockaded woodpecker: notes on life history and management. U.S. Forest Service, Southern Region General Report SA-GR 9.

Hooper, R. G., and M. R. Lennartz. 1981. Foraging behavior of the red-cockaded woodpecker in South Carolina. Auk 98:321-334.

Hooper, R. G., L. J. Niles, R. F. Harlow, and G. W. Wood. 1982. Home ranges of red-cockaded woodpeckers in coastal South Carolina. Auk 99:675-682.

Hooper, R. G. 1983. Colony formation by red-cockaded woodpeckers: hypotheses and management implications. Pages 72-77 *in* D. A. Wood, editor. Red-cockaded woodpecker symposium II proceedings. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.

Hooper, R. G., and R. F. Harlow. 1986. Forest stands selected by foraging red-cockaded woodpeckers. U.S. Forest Service Research Paper SE-259.

Hooper, R. G. 1988. Longleaf pines used for cavities by red-cockaded woodpeckers. Journal of Wildlife Management 52:392-398.

Hooper, R. G., J. C. Watson, and R. E. F. Escano. 1990. Hurricane Hugo's initial effects on red-cockaded woodpeckers in the Francis Marion National Forest. Transactions of the 55th North American Wildlife and Natural Resources Conference 55:220-224.

Hooper, R. G., M. R. Lennartz, and H. D. Muse. 1991. Heart rot and cavity tree selection by red-cockaded woodpeckers. Journal of Wildlife Management 55:323-327.

Hooper, R. G., and C. J. McAdie. 1995. Hurricanes and the long-term management of the red-cockaded woodpecker. Pages 148-166 *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 University, Nacogdoches, Texas, USA.

Hooper, R. G. 1996. Arthropod biomass in winter and the age of longleaf pines. Forest Ecology and Management 82:115-131.

Hooper, R. G., W. E. Taylor, and S. C. Loeb. 2004. Long-term efficacy of artificial cavities for red-cockaded woodpeckers: lessons learned from Hurricane Hugo. Pages 430-438 *in* R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

Hopkins, M. L., and T. E. Lynn, Jr. 1971. Some characteristics of red-cockaded woodpecker cavity trees and management implications in South Carolina. Pp. 140-169 in R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bureau of Sport Fishing and Wildlife and Tall Timbers Research Station, Tallahassee, FL.

Hovis, J. A., and R. F. Labisky. 1985. Vegetative associations of red-cockaded woodpecker colonies in Florida. Wildlife Society Bulletin 13:307-314.

Hoyle, Z. 2008. Red-cockaded woodpeckers and hurricanes. Compass, Southern Research Station, U. S. Forest Service (12):11-13.

Jackson, J. A. 1970. Predation of a black rat snake on yellow-shafted flicker nestlings. Wilson Bulletin 82:329-330.

Jackson, J. A. 1971. The evolution, taxonomy, distribution, past populations, and current status of the red-cockaded woodpecker. Pp. 4-29 in R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bureau of Sport Fishing and Wildlife and Tall Timbers Research Station, Tallahassee, FL.

Jackson, J. A. 1974. Gray rat snakes versus red-cockaded woodpeckers: predator-prey adaptations. Auk 91:342-347.

Jackson, J. A. 1976. How to determine the status of a woodpecker nest. Living Bird Quarterly 15:205-221.

Jackson, J. A. 1977. Red-cockaded woodpeckers and pine red heart disease. Auk 94:160-163.

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

Jackson, J. A. 1978b. Competition for cavities and red-cockaded woodpecker management. Pages 103-112 *in* S. A. Temple, editor. Endangered birds: management techniques for the preservation of threatened species. University Wisconsin Press, Madison, Wisconsin, USA.

Jackson, J. A. 1978c. Analysis of the distribution and population status of the red-cockaded woodpecker. Pages 101-111 *in* R. R. Odum, and L. Landers, editors. Proceedings of the rare and endangered wildlife symposium. Georgia Department of Natural Resources, Game and Fish Division Technical Bulletin W44.

Jackson, J. A. 1979. Age characteristics of red-cockaded woodpeckers. Bird Banding 50:23-29.

Jackson, J. A., M. R. Lennartz, and R. G. Hooper. 1979. Tree age and cavity initiation by red-cockadedwoodpeckers. Journal of Forestry 77:102-103.

Jackson, J. A. 1982. Capturing woodpecker nestlings with a noose - a technique and its limitations. North American Bird Bander 7:90-92.

Jackson, J. A., and B. J. S. Jackson. 1986. Why do red-cockaded woodpeckers need old trees? Wildlife Society Bulletin 14:318-322.

Jackson, J. A., R. N. Conner, and B. J. S. Jackson. 1986. The effects of wilderness on the endangered red-cockaded woodpecker. Pp. 71-78 in D. L. Kulhavy and R. N Conner, eds. Wilderness and natural areas in the eastern United States: a management challenge. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, TX.

Jackson, J. A. 1994. Red-cockaded woodpecker (Picoides borealis). In A. Poole and F. Gill, eds. The birds of North America, No. 85. Academy of Natural Sciences, Philadelphia PA, and the

American Ornithologists' Union, Washington D.C.

James, F. C. 1995. The status of the red-cockaded woodpecker in 1990 and the prospect for recovery. Pp. 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, Stephen F. Austin State University, 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. Ecological Applications 7:118-129.

James, F. C., C. A. Hess, B. C. Kicklighter, and R. A. Thum. 2001. Ecosystem management and the niche gestalt of the red-cockaded woodpecker in longleaf pine forests. Ecological Applications 11:854-870.

Jennings, M. D., D. Faber-Langendon, O. L. Loucks, R. K. Peet, and D. Roberts. 2009. Standards for associations and alliances of the U. S. National Vegetation Classification. Ecological Monographs 79:173-199.

Jones, C. M. 1994. Foraging habitat of the red-cockaded woodpecker on the D'Arbonne National Wildlife Refuge. M.Sc. thesis, Louisiana Tech University, Baton Rouge, LA.

Jones, C. M., and H. E. Hunt. 1996. Foraging habitat of the red-cockaded woodpecker on the D'Arbonne National Wildlife Refuge, Louisiana. Journal of Field Ornithology 67:511-518.

Jones, S. 1989. The implications of Hurricane Hugo on the recovery of the red-cockaded woodpecker. Endangered Species Update 7:6.

Judson, O. P. 1994. The rise of the individual-based model in ecology. Trends in Recent Ecology and Evolution 9:9-14.

Jusino, M. A., D. L. Lindner, M. T. Banik, and J. R. Walters. 2015. Heart rot hotel: fungal communities in red-cockaded woodpecker excavations. Fungal Ecology 14:33-43.

Jusino, M. A., D. L. Lindner, M. T. Banik, K. R. Rose, and J. R. Walters. 2016. Experimental evidence of a symbiosis between red-cockaded woodpeckers and fungi. Proceedings of the Royal Society B Biological Sciences 283:2016.0106

Kalisz, P. J., and S. E. Boettcher. 1991. Active and abandoned red-cockaded woodpecker habitat in Kentucky. Journal of Wildlife Management 55:146-154.

Kane, J. M., J. M. Varner, and J. K. Hiers. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. Forest Ecology and Management 256:2039-2045.

Kelly, J. F., S. M. Pletschet, and D. M. Leslie. 1993. Habitat associations of red-cockaded woodpecker cavity trees in an old growth forest of Oklahoma. Journal of Wildlife Management 57:122-128.

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.

Kappes, J. J., Jr., and J. M. Davis. 2008. Evidence of positive indirect effects within a community of cavity-nesting vertebrates. Condor 110:441-449.

Kappes, J. J., Jr., and K. E. Sieving. 2011. Resin-barrier maintenance as a mechanism of differential predation among occupants of red-cockaded woodpecker cavities. The Condor 113:362-371.

Kesler, D. C., J. R. Walters, and J. J. Kappes. 2010. Social influences on dispersal and the fat-tailed dispersal distribution in red-cockaded woodpeckers. Behavioral Ecology 21:1337-1343.

Khan, M. I., and J. R. Walters. 2002. Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). Behavioral Ecology and Sociobiology 51:336-344.

Koenig, W. D., W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. Quarterly Review of Biology 67:111-150.

Koenig, W. D., and J. R. Walters. 1999. Sex-ratio selection in species with helpers at the nest: the repayment model revisited. American Naturalist 153:124-130.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society Special Publication 36.

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 Bulletin 106:258-271.

Lande, R. 1994. Risk of population extinction from fixation of new deleterious alleles. Evolution 48:1460-1469.

Lande, R. 1995. Mutation and conservation. Conservation Biology 9:782-791.

Landers, J. L. 1991. Disturbance influences on pine traits in the southeastern United States. Pp. 61-98 in S. M. Hermann, ed. High-intensity fire in wildlands: management challenges and options. Tall Timbers Fire Ecology Conference Proceedings, No. 17. Tall Timbers Research Station, Tallahassee, FL.

Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the southeast: requiem or renaissance? Journal of Forestry 93(11):39-44.

Landers, J. L., and W. D. Boyer. 1999. An old growth definition for upland longleaf and south Florida slash pine forests, woodlands, and savannas. USDA Forest Service General Technical Report SRS-29.

Lankau, R.A. 2011. Rapid Evolutionary Change and the Coexistence of Species. Annu. Rev. Ecol. Evol. Syst. 42:335–54.

Laves, K. 1996. Effects of southern flying squirrels, *Glaucomys volans*, on red-cockaded woodpecker, *Picoides borealis,* reproductive success. Thesis, Clemson University, Clemson, South Carolina, USA.

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

Leary, R. F., and F. W. Allendorf. 1989. Fluctuation asymmetry as an indicator of stress: implications for conservation biology. Trends in Recent Ecology and Evolution 4:214-217.

Lennartz, M. R., and R. F. Harlow. 1979. The role of parent and helper red-cockaded woodpeckers at the nest. Wilson Bulletin 91:331-335.

Lennartz, M. R., H. A. Knight, J. P. McClure, and V. A. Rudis. 1983. Status of the red-cockaded woodpecker nesting habitat in the south. Pages 13-19 *in* D. A. Wood, editor. Red-cockaded woodpecker symposium II proceedings. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.

Lennartz, M. R., and D. G. Heckel. 1987. Population dynamics of a red-cockaded woodpecker population in Georgia Piedmont loblolly pine habitat. Pages 48-55 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the third southeastern nongame and endangered wildlife symposium. Georgia Department Natural Resources, Game and Fish Division, Atlanta, Georgia, USA.

Lennartz, M. R., R. G. Hooper, and R. F. Harlow. 1987. Sociality and cooperative breeding of red-cockaded woodpeckers (*Picoides borealis*). Behavioral Ecology and Sociobiology 20:77-88.

Lessells, C. M., and M. I. Avery. 1987. Sex-ratio selection in species with helpers at the nest: some extensions of the repayment model. American Naturalist 129:610-620.

Letcher, B. H., J. A. Priddy, J. R. Walters, and L. B. Crowder. 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. Biological Conservation 86:1-14.

Ligon, J. D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopus* woodpeckers. Auk 85:203-215

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

Ligon, J. D., P. B. Stacey, R. N. Conner, C. E. Bock, and C. S. Adkisson. 1986. Report of the American Ornithologists' Union Committee for the conservation of the red-cockaded woodpecker. Auk 103:848-855.

Lipscomb, D. J., and T. M. Williams. 1995. Impact of Hurricane Hugo on cavity trees of a red-cockaded woodpecker population and natural recovery after two and a half years. Pages 167-171 *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 University, Nacogdoches, Texas, USA.

Liu, K., H. Lu, and C. Shen. 2008. A 1200-year proxy record of hurricanes and fires from the Gulf of Mexico coast: testing the hypothesis of hurricane-fire interactions. Quaternary Research 69:29-41.

Locke, B. A., R. N. Conner, and J. C. Kroll. 1983. Factors influencing colony site selection by red-cockaded woodpeckers. Pp. 46-50 in D. A. Wood, ed. Red-cockaded woodpecker symposium II. Florida Game and Fresh Water Fish Commission, Tallahassee, FL.

Loeb, S. C., W. D. Pepper, and A. T. Doyle. 1992. Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. Southern Journal of Applied Forestry 16:120-125.

Loeb, S. C. 1993. Use and selection of red-cockaded woodpecker cavities by southern flying squirrels. Journal of Wildlife Management 57:329-335.

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

Lohr, S. M. 2004. Red-cockaded woodpecker recovery efforts in an isolated and small South Carolina Sandhills population. Pages 373-377 in R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

Loope, L., M. Duever, A. Herndon, J. Snyder, and D. Jansen. 1994. Hurricane impact on uplands and freshwater swamp forest: large trees and epiphytes sustained the greatest damage during Hurricane Andrew. Bioscience 44:238-246.

Lopez, J. M. G. 2008. Assessing impact of Hurricane Rita on red-cockaded woodpecker

(*Picoides borealis*) clusters in Angelina National Forest, Texas. Thesis, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Lorio, P. L., Jr. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. Forest Ecology and Management 14:259-273.

Lotter, D. M. 1997. Factors influencing southern flying squirrel use of red-cockaded woodpecker cavities at Savannah River Site, S.C. Thesis, Clemson University, Clemson, South Carolina, USA.

Lowery, G. H., Jr. 1960. Louisiana birds. Louisiana State University Press, Baton Rouge, LA.

Lowery, L., and J. Perkins. 2002. Long dispersal of a red-cockaded woodpecker in central Florida. Florida Field Naturalist 30:42-43.

Lynch, M., J. Conery, and R. Burger. 1995. Mutation accumulation and the extinction of small populations. American Naturalist 146:489-518.

Lynch, M., and R. Lande. 1998. The critical effective size for a genetically secure population. Animal Conservation 1:70-72.

Macey, J. N., D. B Burt, D. Saenz, and R. N. Conner. 2016. Habitat use and avoidance by foraging red-cockaded woodpeckers in east Texas. Southeastern Naturalist 15 (Special Issue 9):76-89.

Maguire, L. A., G. F. Wilhere, and Q. Dong. 1995. Population viability analysis for red-cockaded woodpeckers in the Georgia Piedmont. Journal of Wildlife Management 59:533-542.

Martin, T. E., and P. Li. 1992. Life history traits of open vs. cavity-nesting birds. Ecology 73:579-592.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.

Martin, W. H., and S. G. Boyce. 1993. Introduction: the southeastern setting. Pp. 1-46 in W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds. Biodiversity of the southeastern United States: lowland terrestrial communities. John Wiley and Sons, Inc., New York, NY.

Masters, R. E., J. E. Skeen, and J. A. Garner. 1989. Red-cockaded woodpecker in Oklahoma: an update of Wood's 1974-77 study. Proceedings of the Oklahoma Academy of Science 69:27-31.

Masters, R. E., J. Skeen, and J. Whitehead. 1995. Preliminary fire history of McCurtain County Wilderness Area and implications for red-cockaded woodpecker management. Pages 290-302 *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 University, Nacogdoches, Texas, USA.

McDonald, D. B., and H. Caswell. 1992. Matrix models for avian demography. Current Ornithology 10:255-278.

McKellar, A.E., D.C. Kesler, R.J. Mitchell, D.K. Delaney, and J.R. Walters. 2014. Geographic variation in fitness and foraging habitat quality in an endangered bird. Biological Conservation 175:52-64.

McWilliams W.H. 1992. Forest resources of Alabama. Resource Bulletin SO-170. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 71 p.

Meanly, B. 1943. Red-cockaded woodpecker breeding in Maryland. Auk 60:105.

Meffe, G. K., and C. R. Carroll. 1997. Principles of conservation biology. Second edition. Sinauer Associates, Sunderland, MA.

Melillo, J. M. 2014. Climate change impacts in the United States: the third national climate assessment. U.S. Global Change Research Program. Government Printing Office.

Mengel, R. M. 1965. Birds of Kentucky. Ornithological Monograph No. 3, American Ornithologists Union, Washington DC.

Mengel, R. M., and J. A. Jackson. 1977. Geographic variation of the red-cockaded woodpecker. Condor 79:349-355.

Miller, M. P., J. T. Vilstrup, T. D. Mullins, W. McDearman, J. R. Walters, and S. M. Haig. In press. Changes in genetic diversity and differentiation in red-cockaded woodpecker (*Dryobates borealis*) over the past century. Ecology and Evolution.

Mills, L. M., K. J. Feltner, and T. O. Reed. 2004. The rise and fall of the red-cockaded woodpecker population in Kentucky: a chronology of events preceding extirpation. Pages 392-402 *in* R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Conservation Biology 10:1509-1518.

Mitchell, J. H., D. L. Kulhavy, R. N. Conner, and C. M. Bryant. 1991. Susceptibility of red-cockaded woodpecker colony areas to southern pine beetle infestation in east Texas. Southern Journal of Applied Forestry 15:158-162.

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

Mitchell, R. J., and S. L. Duncan. 2009. Range of variability in southern coastal plain forests: its historical, contemporary, and future role in sustaining biodiversity. Ecology and Society 14(1): 17.

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, editors. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Moody, A., N. Haddad, W. F. Morris, and J. Walters. 2011. Mapping habitat connectivity for multiple rare, threatened, and endangered species on and around military installations. Final Report, SERDP Project RC-1471. Strategic Environmental Research and Development Program, Arlington, Virginia, USA.

Murphy, G. A. 1982. Status, nesting habitat, foraging ecology, and home range of the red-cockadedwoodpecker (*Picoides borealis*) in Kentucky. M.Sc. thesis, Eastern Kentucky University,Richmond, KY.

Myers, R. L. and J. J. Ewel, eds. 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida.

Myers, R. K., and D. H. Van Lear. 1998. Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. Forest Ecology and Management, v. 103, p. 265-276.

Myers, R. K., K. J. Hofeldt, and D. H. Van Lear. 1998. Constraints to using fire after Hurricane Hugo to restore fire-adapted ecosystems in South Carolina. Pages 167-172 *in* T. L. Pruden and L. Brennan, eds. Fire in ecosystem management: shifting the paradigm from suppression to prescription. 20th Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, FL.

National Research Council. 1995. Science and the Endangered Species Act. Committee on Scientific Issues in the Endangered Species Act. National Academy of Sciences, National Academies Press. Washington, DC.

Neal, J. C. 1992. Factors affecting breeding success of red-cockaded woodpeckers in the Ouachita National Forest, Arkansas. M.Sc. thesis, University of Arkansas, Fayetteville AR.

Neal, J. C., D. A. James, W. G. Montague, and J. E. Johnson. 1993a. Effects of weather and helpers on survival of nestling red-cockaded woodpeckers. Wilson Bulletin 105:666-673.

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

Neal, J. C., W. G. Montague, D. M. Richardson, and J. H. Withgott. 1998. Exclusion of rat snakes from red-cockaded woodpecker cavities. Wildlife Society Bulletin 26:851-854.

Nebeker, T. E., and J. D. Hodges. 1985. Thinning and harvesting practices to minimize site and stand disturbances and susceptibility to bark beetle and disease attacks. Pp. 263-271 in S. J. Branham and R. C. Thatcher, eds. Proceedings of the integrated pest management research symposium. USDA Forest Service General Technical Report SOH-56.

Nesbitt, S. A., D. T. Gilbert, and D. B. Barbour. 1978. Red-cockaded woodpecker fall movements in a Florida flatwoods community. Auk 95:551-561.

Nesbitt, S. A., E. A. Jerauld, and B. A. Harris. 1983. Red-cockaded woodpecker summer range sizes in southwest Florida. Pages 68-71 *in* D. A. Wood, editor. Red-cockaded woodpecker symposium II proceedings. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.

Neumann, C. J., 1987: The National Hurricane Center risk analysis program (HURISK). NOAA Tech. Memo NWS NHC 38, 56 pp.

Noel, J. M., W. J. Platt, and E. B. Moser. 1998. Structural characteristics of old- and second-growth stands of longleaf pine (*Pinus palustris*) in the Gulf coastal region of the U.S.A. Conservation Biology 12:533-548.

Noss, R.F., E.T. LaRoe III, and J.M. Scott. 1995. Endangered Ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28. U.S. Department of the Interior, National Biological Service.

Omernik, J. M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American Geographers 77:118-125.

Omernik, J. M. and G. E. Griffith. 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54:1249-1266.

Parisi, F. and R. Lund. 2008. Return periods of continental U.S. hurricanes. J. Climate 21:403-410.

Pasinelli, G., and J. R. Walters. 2002. Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. Ecology 83:2229-2239.

Pasinelli, G., K. Schiegg, and J. R. Walters. 2004. Genetic and environmental influences on natal dispersal distance in a resident bird species. The American Naturalist 164:660-669.

Patterson, G. A., and W. B. Robertson, Jr. 1981. Distribution and habitat of the red-cockaded woodpecker in Big Cypress National Preserve. South Florida Research Center Report T-613, Everglades National Park, Homestead, FL.

Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. Pp. 45-82 *in* S. M. Hermann, ed. The longleaf pine ecosystem: ecology, restoration, and management. Tall Timbers Fire Ecology Conference Proceedings, No. 18. Tall Timbers Research Station, Tallahassee, FL.

Peet, R. K. 2006. Ecological classification of longleaf pine woodlands. Pp. 51-94 *in* S. Jose *et al.* eds. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer-Verlag, New York.

Peet, R. K., W. J. Platt, and J. K. Costanza. 2018. Fire-maintained pine savannas and woodlands of the southeastern Coastal Plain. Pages 39-62 *in* A. M. Barton and W. S. Keeton, editors. Ecology and recovery of eastern old growth forests. Island Press, Washington D.C.

Perkins, J. L. 2006. Effects of military training activity on red-cockaded woodpecker and demography, and new territory formation in the cooperatively breeding red-cockaded woodpecker. Thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Phillips, L. F., Jr., J. Tomcho, Jr., and J. R. Walters. 1998. Double-clutching and double-brooding in red- cockaded woodpeckers in Florida. Florida Field Naturalist 26:109-140.

Pizzoni-Ardemani, A. 1990. Sexual dimorphism and geographic variation in the red-cockaded woodpecker (*Picoides borealis*). Thesis, North Carolina State University, Raleigh.

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

Porter, M. L., and R. F. Labisky. 1986. Home range and foraging habitat of red-cockaded woodpeckers in northern Florida. Journal of Wildlife Management 50:239-247.

Provencher, L., H. L. Rogers, K. E. M. Galley, J. L. Hardesty, G. W. Tanner, D. R. Gordon, J. P. McAdoo, J. Sheehan, and L. A. Brennan. 1997. Initial post-treatment analysis of restoration effects on plants, invertebrates, and birds in sandhill systems at Eglin Air Force Base, Florida. Annual Report to Natural Resources Division, Eglin Air Force Base, Niceville, FL.

Provencher, L., K. E. M. Galley, B. J. Herring, J. Sheehan, N. M. Gobris, D. L. Gordon, G. W. Tanner, J. L. Hardesty, H. L. Rodgers, J. P. McAdoo, M. N. Northrup, S. J. McAdoo, and L. A. Brennan. 1998. Post-treatment analysis of restoration effects on soils, plants, arthropods, and birds in sandhill systems at Eglin Air Force Base, Florida. Annual report to Natural Resources Division, Eglin Air Force Base, Niceville, Florida. Public Lands Program, The Nature Conservancy, Gainesville, FL.

Provencher, L., A. R. Litt, K. E. M. Galley, D. R. Gordon, G. W. Tanner, L. A. Brennan, N. M. Gobris, S. J. McAdoo, J. P. McAdoo, and B. J. Herring. 2001a. Restoration of fire-suppressed longleaf pine sandhills at Eglin Air Force Base, Florida. Final report to the Natural Resources Management Division, Eglin Air Force Base, Niceville, Florida. Science Division, The Nature Conservancy, Gainesville, FL.

Provencher, L., B. J. Herring, D. R. Gordon, H. L. Rodgers, K. E. M. Galley, G. W. Tanner, J. L. Hardesty, and L. A. Brennan. 2001b. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restoration Ecology 9:13-27.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Ragheb, E. L. H. and J. R. Walters. 2011. Favouritism or intrabrood competition? Access to food and the benefits of philopatry for red-cockaded woodpeckers. Animal Behaviour 82:329-338.

Ramey, P. 1980. Seasonal, sexual, and geographical variation in the foraging ecology of the red-cockaded woodpecker (*Picoides borealis*). Thesis, Mississippi State University, Mississippi State, USA.

Reed, J. M., J. H. Carter, III, J. R. Walters, and P. D. Doerr. 1988a. An evaluation of indices of red-cockaded woodpecker populations. Wildlife Society Bulletin 16:406-410.

Reed, J. M., P. D. Doerr, and J. R. Walters. 1988b. Minimum viable population size of the red-cockaded woodpecker. Journal of Wildlife Management 52:385-391.

Reed, J. M., J. R. Walters, T. E. Emigh, and D. E. Seaman. 1993. Effective population size in red-cockaded woodpeckers: population and model differences. Conservation Biology 7:302-308.

Reed, J. M., and J. R. Walters. 1996. Helper effects in variance components of fitness in the cooperatively breeding red-cockaded woodpecker. Auk 113:608-616.

Repasky, R. R. 1984. Home range and habitat utilization of the red-cockaded woodpecker. M.Sc. thesis, North Carolina State University, Raleigh, NC.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

Ross, W. G., D. L. Kulhavy, and R. N. Conner. 1995. Vulnerability and resistance of red-cockaded woodpecker cavity trees to southern pine beetles in Texas. Pages 410-414 *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 University, Nacogdoches, Texas, USA.

Ross, W. G., D. L. Kulhavy, and R. N. Conner. 1997. Stand conditions and tree characteristics affect quality of longleaf pine for red-cockaded woodpecker cavity trees. Forest Ecology and Management 91:145-154.

Rossell, C. R., Jr., and J. J. Britcher. 1994. Evidence of plural breeding by red-cockaded woodpeckers. Wilson Bulletin 106:557-559.

Rossell, C. R., Jr., and B. Gorsira. 1996. Assessment of condition and availability of active red-cockaded woodpecker cavities. Wildlife Society Bulletin 24:21-24.

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 Bulletin 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 Bulletin 102:14-22.

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

Rudolph, D. C., and R. N. Conner. 1994. Forest fragmentation and red-cockaded woodpecker population: an analysis at intermediate scale. Journal of Field Ornithology 65:365-375.

Rudolph, D. C., and R. N. Conner. 1995. The impact of southern pine beetle induced mortality on red-cockadedwoodpecker cavity trees. Pp. 208-213 in D. L. Kulhavy, R. G. Hooper, and R. Costa,eds. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, TX.

Rudolph, D. C., R. N. Conner, and R. R. Schaefer. 1995. Red-cockaded woodpecker detection of red heart infection. Pp. 338-342 in D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology, and management. Center for Applied Studies in Forestry, Stephen F. Austin State University, Nacogdoches, TX.

Rudolph, D. C., R. N. Conner, and J. R. Walters. 2004. Red-cockaded woodpecker recovery: an integrated strategy. Pages 70-76 in R. Costa, and S. J. Daniels, editors. Red-cockaded woodpecker: road to recovery. Hancock House, Blaine, Washington, USA.

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

Saenz, D., R. N. Conner, C. S. Collins, and D. C. Rudolph. 2001. Initial and long-term use of inserts by red-cockaded woodpeckers. Wildlife Society Bulletin 29:165-170.

Sanders, F. J. 2000. Brood reduction and the insurance hypothesis as explanations for asynchronous hatching in red-cockaded woodpeckers. M.Sc. thesis, Clemson University, Clemson, SC.

Schaeffer, R. R., Jr. 1996. Red-cockaded woodpecker reproduction and provisioning of nestlings in relation to habitat. Thesis, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Schaefer, R. R., R. N. Conner, D. C. Rudolph, and D. Saenz. 2004. Red-cockaded woodpecker nestling provisioning and reproduction in two different pine habitats. Wilson Bulletin 116:31-40.

Schiegg, K., G. Pasinelli, J.R. Walters, and S. J. Daniels. 2002. Inbreeding and experience affect response to climate change by endangered woodpeckers. Proceedings of the Royal Society Biological Sciences 269:1153-1159.

Schiegg, K., J. R. Walters, and J. A. Priddy. 2005. Testing a spatially explicit, individual-based model of red-cockaded woodpecker population dynamics. Ecological Applications 15:1495-1503.

Schiegg, K., S. J. Daniels, J. R. Walters, J. A. Priddy, and G. Pasinelli. 2006. Inbreeding in red-cockaded woodpeckers: effects of natal dispersal distance and territory location. Biological Conservation 131:544-552.

Schrott, G. R., L. Gilson, and R. Bowman. 2010. Differential reproductive success in a red-cockaded woodpecker population: implications for hatch failure rates. Abstract. Ecological Society of America, 95th Annual Meeting, Pittsburg.

Shakya, S. B., J. Fuchs, J. M. Pons, and F. H. Sheldon. 2017. Tapping the woodpecker tree for evolutionary insight. Molecular Phylogenetics and Evolution 116:182-191.

Shapiro, A. E. 1983. Characteristics of red-cockaded woodpecker cavity trees and colony areas in southern Florida. Florida Scientist 46:89-95.

Short, L. L. 1982. Red-cockaded woodpecker, *Picoides borealis*. Pages 308-314 *in* Woodpeckers of the world. Delaware Museum of Natural History, Greenville, Delaware, USA.

Simberloff, D. 1993. Species-area and fragmentation effects on old growth forests: prospects for longleaf pine communities. Pp. 1-14 *in* S. M. Hermann, ed. The longleaf pine ecosystem: ecology, restoration, and management. Tall Timbers Fire Ecology Conference Proceedings, No. 18. Tall Timbers Research Station, Tallahassee, FL.

Smith, E., and R. Martin. 1995. Red-cockaded woodpecker distribution and status in Louisiana. Pages 452-456 *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 University, Nacogdoches, Texas, USA.

Smith, D. R., N. L. Allan, C. P. McGowan, J. A. Szymanski, S. R. Oetker, and H. M. Bell. 2018a. Development of a species status assessment process for decisions under the U.S. Endangered Species Act. Journal of Fish and Wildlife Management 9:302-320.

Smith, J. A., J. H. Carter III, J. Goodson, A. Jackson, M. King, J Kolts, and J. R. Walters. 2018b. Potential contribution of Dare County Bombing Range to the red-cockaded woodpecker population in eastern North Carolina. U.S. Fish and Wildlife Service-Virginia Tech Cooperative Agreement F15AC00089. Report to U. S. Fish and Wildlife Service, Atlanta, GA.

Society for Ecological Restoration Science and Policy Working Group. 2002. The SER primer on ecological restoration. www.ser.org/.

Sorrie, B. A. and A. S. Weakley. 2006. Conservation of the endangered *Pinus palustris* ecosystem based on Coastal Plain centres of plant endemism. Applied Vegetation Science 9:59-66.

Stacey, P. B., and J. D. Ligon. 1991. The benefits of philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. American Naturalist 137:831-846.

Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18-29.

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

Stangel, P. W., and P. M. Dixon. 1995. Associations between fluctuating asymmetry and heterozygosity in the red-cockaded woodpecker. Pages 225-226 *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 University, Nacogdoches, Texas, USA.

Steirly, C. C. 1957. Nesting ecology of the red-cockaded woodpecker in Virginia. Raven 28:24-36.

Steirly, C. C. 1973. Red-cockaded woodpeckers on the Piedmont. Raven 44:80.

Stith, B. M., J. W. Fitzpatrick, G. E. Woolfenden, and B. Pranty. 1996. Classification and conservation of metapopulations: a case study of the Florida Scrub Jay. Pp. 187-215 *in* D. R. McCullough, ed. Metapopulations and wildlife conservation. Island Press, Washington DC.

Sutton, G. M. 1967. Oklahoma birds. University of Oklahoma Press, Norman, OK.

Taylor, W. E., and R. G. Hooper. 1991. A modification of Copeyon's drilling technique for making artificial red-cockaded woodpecker cavities. USDA Forest Service General Technical Report SE-72.

Templeton, A. R., H. Hemmer, G. Mace, U. S. Seal, W. M. Shields, and D. S. Woodruff. 1986. Local adaptation, coadaptation, and population boundaries. Zoo Biology 5:115-125.

Thatcher, R. C., J. L. Searcy, J. E. Coster, and G. D. Hertel, eds. 1980. The southern pine beetle. USDA Forest Service, Science Education Administration Technical Bulletin 1631.

The Nature Conservancy. 2002. Upper West Gulf Coastal Plain ecoregional plan.

Thompson, R. L., and W. W. Baker. 1971. A survey of red-cockaded woodpecker requirements. Pp. 170-186 in R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bureau of Sport Fishing and Wildlife and Tall Timbers Research Station, Tallahassee, FL.

Trainor, A. M., J. R. Walters, W. F. Morris, J. Sexton, and A. Moody. 2013. Empirical estimation of dispersal resistance surfaces: a case study of red-cockaded woodpeckers.

Landscape Ecology 28:755-767.

Trepanier, J. C. and K. N. Scheitlin. 2014. Hurricane wind risk in Louisiana. Natural Hazards 70: 1181–1195.

U.S. Army. 1996. Management guidelines for the red-cockaded woodpecker on Army installations. U.S. Department of the Army, Washington, D.C.

U.S. Federal Geographic Data Committee. 2008. National Vegetation Classification Standard. Version 2.0. https://www.fgdc.gov/standards/projects/vegetation/NVCS_V2_FINAL_2008-02.pdf.

U.S. Fish and Wildlife Service. 1985. Red-cockaded woodpecker recovery plan. Southeast Region, Atlanta, GA.

U.S. Fish and Wildlife Service. 1989. Guidelines for preparation of biological assessments and evaluations for the red-cockaded woodpecker. Atlanta, GA.

U.S. Fish and Wildlife Service. 1998. Endangered species consultation handbook: procedures for conducting consultation and conference activities under Section 7 of the Endangered Species Act. U. S. Fish and Wildlife Service and National Marine Fisheries Service. Washington DC.

U.S. Fish and Wildlife Service. 2003. Red-cockaded Woodpecker (*Picoides borealis*) Recovery Plan: *Second Revision*. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

U.S. Fish and Wildlife Service. 2016. USFWS Species Status Assessment Framework: an integrated analytical framework for conservation. Version 3.4 dated August 2016.

U.S. Forest Service. 1995. Final environmental impact statement for the management of the red-cockaded woodpecker and its habitat on national forests in the southern region. U.S. Forest Service Management Bulletin R8-MB 73 (3 volumes).

U.S. National Vegetation Classification. 2017. Database, V2.01. Federal vegetation geographic committee, vegetation committee. Washington, D.C.

Van Balen, J. B. and P. D. Doerr. 1978. The relationship of understory vegetation to red-cockaded woodpecker activity. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 32:82-92.

Vieillot, L. J. P. 1807. Historie naturelle des oiseaux de l’Amerique septrionale. 2:66. Chez Desray, Paris, France.

Wahlenburg, W. G. 1946. Longleaf pine: its use, ecology, regeneration, protection, growth, and management. Charles Lothrop Pack Forestry Foundation and USDA Forest Service, Washington, D.C.

Walker, J. L., and R. K. Peet. 1983. Composition and species diversity of pine-wiregrass savannahs of the Green Swamp, North Carolina. Vegetatio 55:163-179.

Walker, J. L. 1993. Rare vascular plant taxa associated with the longleaf pine. Pp. 227-263 *in* S. M. Hermann, ed. The longleaf pine ecosystem: ecology, restoration, and management. Tall Timbers Fire Ecology Conference Proceedings, No. 18. Tall Timbers Research Station, Tallahassee, FL.

Walker, J. L. 1999. Longleaf pine forests and woodlands: old growth under fire! Pp. 33-40 in G. L. Miller, ed. The value of old growth forest ecosystems of the Eastern United States: conference proceedings. University of North Carolina, Asheville, NC.

Walters, E. L. 2004. Estimating species interactions in a woodpecker tree-hole community at the individual, population, and community levels. Dissertation, Florida State University, Tallahassee, USA.

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

Walters, J. R., S. K. Hansen, P. D. Manor, J. H. Carter III, and R. J. Blue. 1988b. Long-distance dispersal of an adult red-cockaded woodpecker. Wilson Bulletin 100:494-496.

Walters, J. R. 1990. The red-cockaded woodpecker: a "primitive" cooperative breeder. Pages 67-101 *in* P. B. Stacey, and W. D. Koenig, editors. Cooperative breeding in birds: long term studies of ecology and behavior. Cambridge University Press, Cambridge, United Kingdom.

Walters, J. R. 1991. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. Annual Review of Ecology and Systematics 22:505-523.

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

Walters, J. R., P. D. Doerr, and J. H. Carter III. 1992b. Delayed dispersal and reproduction as a life history tactic in cooperative breeders: fitness calculations from red-cockaded woodpeckers.

American Naturalist 139:623-643.

Walters, J. R., S. J. Daniels, J. H. Carter, III, P. D. Doerr, K. Brust, and J. M. Mitchell. 2000. Foraging habitat resources, preferences and fitness of red-cockaded woodpeckers in the North Carolina sandhills. Fort Bragg Project Final Report. Virginia Polytechnic Institute and State University, Blacksburg, VA, and North Carolina State University, Raleigh, NC.

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. Journal of Wildlife Management 66:1064-1082.

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

Walters, J. R., T. B. Taylor, S. J. Daniels, L. B. Crowder, and J. A. Priddy. 2002. Current and future dynamics of the red-cockaded woodpecker population inhabiting the Savannah River National Environmental Research Park: managing for population growth. Final project report to USDA Forest Service, The Savannah River Natural Resources Management Institute. New Ellenton, SC.

Walters, J. R., C. B. Cooper, S. J. Daniels, G. Pasinelli, and K. Schiegg. 2004. Conservation biology. Pages 197-209 *in* W. D. Koenig and J. L. Dickinson, editors. Ecology and evolution of cooperative breeding birds. Cambridge University Press.

Walters, J. R. and J. A. Priddy. 2005. Evaluation of red-cockaded woodpecker demographics and conservation planning on Plum Creek lands through simulation modeling. Technical Report. Department of Biology, Virginia Tech University, Blacksburg, Virginia, USA.

Walters, J. R., K. Brust, S. J. Daniels, J. H. Carter, III, K. Schiegg, G. Pasinelli, and P. D. Doerr. 2006. Demographic connections within the Sandhills red-cockaded woodpecker population. Final project report to U. S. Fish and Wildlife Service, Raleigh, NC.

Walters, J. R., P. Baldassaro, K. M. Convery, R. McGregor, L. B. Crowder, J. A. Priddy, D. C. Kessler, and S. A. Tweddale. 2011. A decision support system for identifying and ranking critical habitat parcels on and in the vicinity of Department of Defense installations. Final Report, SERDP Project RC-1472. Strategic Environmental Research and Development Program, Arlington, Virginia, USA.

Walters, J. R. and V. Garcia. 2016. Red-cockaded woodpeckers: alternative pathways to breeding success. Pages 58-76 *in* W. D. Koenig and J. L. Dickinson, editors. Cooperative breeding in vertebrates. Cambridge University Press.

Waples R. S., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Molecular Ecology 15:1419–1439.

Ware, S., C. Frost, and P. D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. Pp. 447-493 in W. H. Martin, S. G. Boyce, and A. C. Echternacht, eds. Biodiversity of the southeastern United States: lowland terrestrial communities. John Wiley and Sons, Inc., New York, NY.

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 University, Nacogdoches, Texas, USA.

Watts, W. A. 1971. Postglacial and interglacial vegetation history of southern Georgia and central Florida. Ecology 52:676-690.

Watts, W. A., B. C. S. Hansen, and E. C. Grimm. 1992. Camel Lake: a 40,000-yr. record of vegetational forest history from northwest Florida. Ecology 73:1056-1066.

Weibel, A.C. and W. S. Moore. 2002a. A test of mitochondrial gene-based phylogeny of woodpeckers (genus *Picoides*) using an independent nuclear gene, β-fibrinogen intron 7. Molecular Phylogenetics and Evolution 22:247-257.

Weibel, A.C. and W. S. Moore. 2002b. Molecular phylogeny of a cosmopolitan group of woodpeckers (genus *Picoides*) based on COI and cyt *b* mitochondrial gene sequenc3es. Molecular Phylogenetics and Evolution 22:65-75.

Wetmore, A. 1941. Notes on the birds of North Carolina. Proceedings of the U.S. National Museum 90:483-530.

White, Z. W. 1984. Loblolly pine with emphasis on its history. Pp. 1-16 *in* B. L. Karr, J. B. Baker, and T. Monaghan, eds. Proceedings of the symposium on the loblolly pine ecosystem (west region). School of Forest Resources, Mississippi State University, Jackson, MS.

Whitlock, M. C. and D. E. McCauley. 1999. Indirect measures of gene flow and migration: $F_{st} \neq 1/(4N_m + 1)$. Heredity 82:117-125.

Williams, T. M., and D. J. Lipscomb. 2002. Natural recovery of red-cockaded woodpecker cavity trees after Hurricane Hugo. Southern Journal of Applied Forestry 26:197-206.

Wilson, A. 1810. American ornithology, Vol. 2. Bradford and Inskeep, Philadelphia, PA.

Wilson, A., and C. L. Bonaparte. 1830. *Picus querulus*, red-cockaded woodpecker. Page 187 *in* American ornithology or the natural history of the birds of the United States. Volume 1. Constable and Company, Edinburgh, England.

Winkler, H., A. Gamauf, F. Nittinger, and E. Haring. 2014. Relationships of old world woodpeckers (Aves: Picidae) – new insights and taxonomic implications. Annalen des Naturhistorischen Museums in Wien B 116:69-86.

Wolf. S., B. Hartl, C. Carroll, M.C. Neel, and D.N. Greenwald. 2015. Beyond PVA: why recovery under the Endangered Species Act is more than population viability. BioScience 65:200-207.

Wood, D. A. 1983. Foraging and colony habitat characteristics of the red-cockaded woodpecker in Oklahoma. Pages 51-58 in D. A. Wood, editor. Red-cockaded woodpecker symposium II proceedings. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.

Wood, D. R., F. J. Vilella, and L. W. Burger Jr. 2008. Red-cockaded woodpecker home range use and macrohabitat selection in a loblolly-shortleaf pine forest. Wilson Journal of Ornithology 120:793-800.

Worton, B. J. 1989. Kernel methods for estimating utilization distribution in home-range studies. Ecology 70:164-168.

Zack, S. and K. N. Rabenold.1989. Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. Animal Behavior 38:235-247.

Zeigler, S. L. and J. R. Walters. 2014. Population models for social species: lessons learned from models of red-cockaded woodpeckers (*Picoides borealis*). Ecological Applications 24:2144-2154.

Zenitsky, F. D. 1999. The foraging behavior of red-cockaded woodpeckers (Picoides borealis) in stands intensively managed for hardwood midstory on the Daniel Boone National Forest, Kentucky. M.Sc. thesis, Eastern Kentucky University, Richmond, KY.

Zwicker, S. M., and J. R. Walters. 1999. Selection of pines for foraging by red-cockaded woodpeckers. Journal of Wildlife Management 63:843-852.