

**THE DYNAMICS OF CAVITY EXCAVATION AND USE BY THE
RED-COCKADED WOODPECKER (*Picoides borealis*)**

by

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(ABSTRACT)

Quantification of cavity excavation produced strong empirical support for the ecological constraints model for the evolution of delayed dispersal in the red-cockaded woodpecker. The long times required for cavity excavation select for competition over breeding vacancies in established territories and against excavation of cavities in unoccupied habitat. Duration of excavation varies between woodpecker populations, but may require over 13 years in longleaf pine and over 10 years in loblolly pine. Duration of excavation is extremely variable. Much of the variation is due to variation in effort by excavating woodpeckers, which is in turn related to the need for new cavities in relation to the number of available cavities on a territory. An average of only 11 % of an individual's time budget is devoted to excavation, and only one individual per group makes significant contributions to excavation. Once completed, cavities are used for periods that may exceed fifteen years. Cavities in longleaf pine are used for significantly longer periods than cavities in loblolly. Whereas cavities no longer used as nests are abandoned altogether in loblolly, they are still roosted in for many years in longleaf. Final abandonment of longleaf cavities appears to be related to cavity loss. Quantification of cavity turnover revealed that three of the study populations (MACK, CNF and CL) were stable in cavity numbers over the study period, while a fourth (FB) underwent alarming declines. The continued use of restrictors and artificial cavities, and the protection of old-growth upon which the woodpeckers depend for excavation, are recommended.

Dedication

I dedicate this thesis to Monica Marie Meyer

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Table of Contents

	Page
LIST OF TABLES	viii
LIST OF FIGURES	xii
PART I: DYNAMICS OF CAVITY EXCAVATION AND USE	1
CHAPTER 1: INTRODUCTION	1
Cavities and the Cooperative Breeding System	1
The Decline and Conservation of the Red-cockaded Woodpecker	4
CHAPTER 2: METHODS	7
Study Area	7
Data Collection	7
Data Analysis: Survival Analysis	10
CHAPTER 3: DYNAMICS OF CAVITY EXCAVATION	12
Methods	12
Timing of Excavation	12
Description of Analyses	12
Criteria for Inclusion of Data into Analyses	13
Survival Analysis	14
Results	15
Duration of the Entire Excavation Process	15
Comparison of Analyses	15
Comparison of Pine Species	21
Comparison of Cavity Populations	22
Duration of the Different Stages of Excavation	24
Comparison of Analyses	24
Comparison of Tree Species	26
Comparison of Cavity Populations	26
Discussion	27
Patterns of Cavity Excavation	27
Cavity Excavation and the Cooperative Breeding System	27
The Stages of Excavation	29
Differences in Duration of Excavation	30
Differences Between Tree Species	31
Differences Between Cavity Populations	32
Duration of Excavation and Survival Analysis	32

CHAPTER 4: DYNAMICS OF CAVITY USE	34
Methods	34
Patterns of Cavity Use	34
Analysis of the Duration of Cavity Use for Roosting and Nesting	35
Description of Analyses	35
Criteria for Inclusion of Data into Analyses	36
Survival Analysis	37
Results	38
Analysis of the Duration of Use of Cavities as Roost Cavities	38
Naturally Excavated Cavities	38
Artificial Cavities	45
Analysis of the Duration of Use of Cavities as Nest Cavities	45
Naturally Excavated Cavities	45
Artificial Cavities	54
Discussion	55
Patterns of Cavity Use	55
Differences in Duration of Use Between Tree Species	58
Differences in Duration of Use Between Cavity Populations	60
Artificial Cavities	61
 CHAPTER 5: CAVITY TURNOVER	 63
Methods	63
Cavity Turnover	63
Cavity Gains	63
Cavity Losses	65
Common Cavities	67
Management Effects	67
Effects on Estimation of Gains and Losses	67
Results	68
Fort Bragg and Camp Mackall	68
Cavity Gains	68
Cavity Losses	70
Cavity Turnover	74
Management Effects on Cavity Turnover	78
Croatan National Forest	79
Cavity Gains	79
Cavity Losses	81
Cavity Turnover	84
Management Effects on Cavity Turnover	85
Camp LeJeune	85
Cavity Gains	85
Cavity Losses	87
Cavity Turnover	90
Management Effects on Cavity Turnover	91
Discussion	91

Cavity Dynamics and Their Underlying Causes	91
Cavity Gains	93
Cavity Losses	93
Cavity Population Management	94
PART II: SOCIAL DYNAMICS OF CAVITY EXCAVATION	97
CHAPTER 6: SOCIAL DYNAMICS OF CAVITY EXCAVATION	97
Introduction	97
Methods	102
Study Area	102
Data Collection	102
Criteria for Inclusion of Woodpecker Groups into Sample	102
Sampling Protocol	102
Differences in Sampling Procedures Between Field Seasons	104
Data Analysis	105
Cavity Excavation	105
Cavity Availability and Cavity Loss	107
Results	108
Excavation Behavior	108
Summary of Excavation Statistics	111
Excavation Over Different Times of Day	111
Excavation by Groups of Different Sizes	112
Excavation by Individuals of Different Status Classes	113
Excavation of Different Cavities	113
Excavation Times	114
Excavational Peck Rates	115
Excavation at the Group Level	116
Excavation at the Individual Level	119
Primary Excavators	121
Excavation by Fledglings	123
Discussion	124
Cavity Excavation	124
Excavation at the Group Level	125
Excavation at the Individual Level	127
CONCLUSIONS	130
LITERATURE CITED	132
APPENDIX	141
VITA	145

List of Tables

Table	Page
3.1. Reactivation rates of cavities excavated in longleaf pine following periods of continuous inactivity of varying lengths	16
3.2. Reactivation rates of cavities excavated in loblolly pine following periods of continuous inactivity of varying lengths	17
3.3. Fate of cavities of non-completed status at the start of and throughout each study on FB/MACK, CNF and CL	17
3.4. Duration in years of cavity excavation from substart/start to completed cavity by the red-cockaded woodpecker	18
3.5. Duration in years of cavity excavation, divided into its component stages, for the analyses of uncensored observations	19
3.6. Duration in years of cavity excavation, divided into its component stages, for the survival analyses	20
3.7. Test results for comparisons between tree species of duration of excavation of stage transitions	21
3.8. Test results for comparisons between cavity populations of duration of excavation of stage transitions	24
3.9. Test results for comparisons of duration of excavation between stage transitions for analyses of uncensored observations and survival analyses	25
3.10. Test results for comparisons of duration of excavation in longleaf pine for those significant differences in the analyses of successfully completed stages	25
3.11. Test results for comparisons of duration of excavation for those significant differences in the analyses using censored observations	26
4.1. Reuse rates of roost cavities following periods of non-use. Includes all cavities suitable for analysis regardless of cavity fate	39
4.2. Reuse rates of roost cavities following periods of non-use. Does not include cavities that were lost	40

4.3. Three representative measures of duration in years of use of cavities for roosting. Includes all cavities suitable for analysis regardless of cavity fate	41
4.4. Statistical test results for comparisons between tree species of duration of use of cavities for roosting	42
4.5. Statistical test results for comparisons between cavity populations of duration of use of cavities for roosting	42
4.6. Three representative measures of duration in years of use of cavities for roosting. Does not include cavities that were lost	43
4.7. Duration in years of continuous use of artificial cavities for roosting. Includes all cavities suitable for analysis regardless of cavity fate	45
4.8. Reuse rates of nest cavities following periods of non-use. Includes all cavities suitable for analysis regardless of cavity fate	46
4.9. Reuse rates of nest cavities following periods of non-use. Does not include cavities that were lost	47
4.10. Three representative measures of duration in years of use of cavities as nests. Includes all cavities suitable for analysis regardless of cavity fate	48
4.11. Statistical test results for comparisons between tree species of duration of use of cavities as nest cavities	49
4.12. Statistical test results for comparisons between cavity populations of duration of use of cavities as nest cavities	49
4.13. Three representative measures of duration in years of use of cavities as nests. Does not include cavities that were lost	50
4.14. Test results for comparisons of duration of use of cavities as nests between all cavities and cavities that remained suitable	51
4.15. Statistical test results for comparisons between tree species of duration of use of cavities as nests for cavities that remained suitable	51
4.16. Duration of use of artificial cavities as nests in longleaf pine by red-cockaded woodpeckers. Includes all cavities regardless of fate	55
4.17. Test results for comparisons of duration of use of cavities as nests between naturally excavated cavities and artificial cavities	55

4.18. Number of cavities used for roosting following periods of various lengths representing the number of years between cavity completion and first use	56
4.19. Number of cavities used for nesting following periods of various lengths representing the number of years between cavity completion and first use	56
5.1. Percentage of cavity gains comprised of suitable, newly discovered cavities	64
5.2. Turnover in completed cavities on FB between 1980 and 1995 by tree species	69
5.3. Turnover in completed cavities on MACK between 1980 and 1995 by tree species	69
5.4. Turnover in completed cavities on CNF between 1988 and 1996 by tree species	79
5.5. Turnover in completed cavities on CL between 1986 and 1996 by tree species	86
5.6. Percentages of trees dying by cause of death	94
6.1. Hypotheses and predictions about the excavation process in red-cockaded woodpeckers	101
6.2. Mean excavational time budgets based on all adult red-cockaded woodpeckers in groups that excavated	106
6.3. Summary statistics of number of pecks per excavational bout	109
6.4. Percentage of sample points within each time block corresponding to excavation events	112
6.5. Percentage of excavating individuals within each helper class for groups that excavated	113
6.6. Mean excavational time budgets based on individual red-cockaded woodpeckers that excavated	115
6.7. Proportion of time that cavities were excavated by groups of different sizes. Includes groups that did and did not excavate	115
6.8. Proportion of time that cavities were excavated by groups of different sizes. Includes groups that excavated only	115

6.9. Mean peck rates of red-cockaded woodpeckers	116
6.10. Mean peck rates of red-cockaded woodpeckers of different status	116
6.11. Proportion of time that cavities were excavated by groups with different cavity to bird ratios, where ratios include male fledglings	117
6.12. Proportion of time that cavities were excavated by groups with different cavity to bird ratios, where ratios do not include fledglings	117
6.13. Proportion of time that cavities were excavated by groups with different yearly cavity loss rates	117
6.14. Percentage of different sized groups with cavity to bird ratios less than and with cavity loss rates greater than zero	118
6.15. Patterns of excavation in groups without helpers	119
6.16. Patterns of excavation in groups with one helper	120
6.17. Patterns of excavation in groups with two helpers	120
6.18. Excavational time budgets of individuals of different status classes in groups with helpers and multiple excavators	121
6.19. Patterns of excavation for primary excavators in groups without helpers	122
6.20. Patterns of excavation for primary excavators in groups with one helper	122
6.21. Patterns of excavation for primary excavators in groups with two helpers	122

List of Figures

Figure	Page
3.1. Percentage distribution of duration of the process of cavity excavation (substart to completed cavity)	23
4.1. Percentage distribution of duration of use of cavities in longleaf pine for roosting	44
4.2. Percentage distribution of duration of continuous use of cavities in longleaf pine for roosting on FB/MACK	45
4.3. Percentage distribution of duration of use of cavities in longleaf pine for nesting	52-53
4.4. Percentage distribution of duration of continuous use of cavities in loblolly pine for nesting on FB/MACK	53
4.5. Percentage distribution of duration of use of cavities in longleaf pine for nesting on FB/MACK	54
5.1. Yearly gains of completed cavities on FB in three tree species	69
5.2. Yearly gains of completed cavities on MACK in three tree species	70
5.3. Numbers of red-cockaded woodpecker groups and gains of completed cavities on FB	71
5.4. Numbers of red-cockaded woodpecker groups and gains of completed cavities on MACK	71
5.5. Cavity gains per group on FB	72
5.6. Cavity gains per group on MACK	72
5.7. Yearly losses of completed cavities on FB in three tree species	73
5.8. Percentage of suitable cavities lost on FB	73
5.9. Percentage of suitable cavities lost on MACK	74
5.10. Causes of cavity loss on FB	75

5.11. Causes of cavity loss on MACK	75
5.12. Percentage of lost cavities that were lost to enlargement and to tree death on FB	76
5.13. Percentage of lost cavities that were lost to enlargement and to tree death on MACK	76
5.14. Rates of gain and of loss of completed cavities on FB	77
5.15. Rates of gain and of loss of completed cavities on MACK	77
5.16. Yearly gains of completed cavities on CNF in three species of tree	80
5.17. Numbers of red-cockaded woodpecker groups and gains of completed cavities on CNF	80
5.18. Cavity gains per group on CNF	81
5.19. Yearly losses of completed cavities on CNF in three tree species	82
5.20. Percentage of suitable cavities lost on CNF	82
5.21. Causes of cavity loss on CNF	83
5.22. Percentage of lost cavities that were lost to enlargement and to tree death on CNF	83
5.23. Rates of gain and of loss of completed cavities on CNF	84
5.24. Yearly gains of completed cavities on CL in three species of tree	86
5.25. Numbers of red-cockaded woodpecker groups and gains of completed cavities on CL	87
5.26. Cavity gains per group on CL	87
5.27. Yearly losses of completed cavities on CL in three tree species	88
5.28. Percentage of suitable cavities lost on CL	88
5.29. Causes of cavity loss on CL	89
5.30. Percentage of lost cavities that were lost to enlargement and to tree death on CL	90

5.31. Rates of gain and of loss of completed cavities on CL	90
6.1 Percentage of groups for which excavation was witnessed within different group size categories	112
6.2. Number of individuals that excavated and that did not excavate within different status classes	114
6.3. Mean peck rates of individuals in different age classes	116

Part I

Chapter 1: Introduction

The red-cockaded woodpecker (*Picoides borealis*) is an inhabitant of the pine forests of the southeastern United States. Once abundant across the Southeast, the bird was placed on the Federal Endangered Species List in 1968 (U.S. Dept. Interior 1968) because of dramatic declines in its natural habitat. These declines are attributable to the depletion, fragmentation and conversion of pine forests by logging practices (Jackson 1994) and development over the bird's entire range. Unlike other North American picids, which excavate cavities for roosting and nesting in dead trees, the red-cockaded woodpecker excavates cavities almost exclusively in living pine trees (Steirly 1957, Hooper 1982). The process of cavity excavation in living trees is fraught with difficulties not encountered excavating in dead wood. As a result, duration of excavation from beginning to end can take several years (Conner and Rudolph 1995a). The cavities that are produced, however, are often used for many years (Ligon 1970, Jackson 1978, Harlow 1983) and have the potential to be used for periods spanning several woodpecker lifetimes (Lay and Russel 1970, Conner and Rudolph 1995a). The woodpecker is also unique among its congeners in being one of three percent of 9000 avian species (Stacey and Ligon 1987) that have been documented as exhibiting a cooperative breeding system, whereby mature individuals defer reproduction and help rear offspring that are not their own (Emlen 1991). Red-cockaded woodpeckers live in groups that typically consist of two to five individuals. In the past decade, a link has been established between the woodpecker cavity and the evolutionary rise of its social system (Walters et al. 1988, Walters 1991, Walters et al. 1992b). The hypothesis contends that the extended time required by the woodpeckers to excavate cavities was a major factor contributing to the evolution of delayed dispersal in this species. The primary objective of Part I of this thesis is the quantification of the duration of cavity excavation by the red-cockaded woodpecker, in order to test the assumption of a high time cost of excavation. Cavity use is also quantified in order to determine the value of completed cavities to the woodpecker, as the cavity has been recognized as a critical resource. The number of existing woodpecker groups in a population in fact depends heavily on the number of territories with suitable cavity trees (Walters 1991). Because of this, the rates at which cavities are constructed and lost are critical to population dynamics and to management of the species. A secondary objective is to document turnover rates of cavities to determine if four populations of cavities in North Carolina are increasing or decreasing.

Cavities and the Cooperative Breeding System

Cooperative breeding systems take two general forms in monogamous avian species: (1) helper-at-the-nest systems, in which each territory is occupied by one breeding pair and their helpers; and (2) the socially more complex plural or communal systems, in which each territory holds more than one breeding pair and their helpers (Emlen 1991). The red-cockaded woodpecker clearly falls within the former category. Alloparental care in the woodpecker is exhibited almost exclusively by male individuals that defer natal dispersal and reproduction. Females, instead, rarely exhibit philopatry (Walters et al. 1988). Natal dispersal is defined here

according to Greenwood and Harvey's (1982) modification of Howard's (1960) definition, as "the permanent movement an individual makes from its birth site to the place where it *first* reproduces or would have reproduced if it had survived and, *for a surviving individual, had it* found a mate (words in italics added)." A genetic relationship commonly exists between a helper and the young it helps to raise. However, cases of individuals helping to rear non-related young have been documented for the species (Walters et al. 1988). The number of helpers on any given territory generally does not exceed two, although groups of woodpeckers with three helpers have been reported (Walters et al. 1988, Jackson 1994). Helping behavior in the woodpecker includes territorial defense (Ligon 1970), incubation (Lay et al. 1971, Lennartz and Harlow 1979), brooding (Ligon 1970, Lennartz and Harlow 1979), pre- (Baker 1971, Ligon 1970, Lennartz and Harlow 1979) and post-fledging provisioning (Ligon 1970), as well as maintenance (Walters, pers. comm.) and construction of cavities (Ligon 1970).

Did cooperative breeding evolve independently in the red-cockaded woodpecker or is it merely a phylogenetic artifact? This social system appears to be unique to *borealis* within the genus *Picoides*, indicating that it likely is a derived character (Ligon 1993). Furthermore, while natal philopatry seems to be well-established in the red-cockaded woodpecker, it is but one of two alternative life history strategies available to male fledglings (Walters et al. 1992a): approximately one half as many fledglings as those dispersing exhibit philopatry (Walters et al. 1988). This contrasts with the cooperative breeding systems of other avian species, in which natal dispersal is rare (Walters, 1990). The woodpecker's social system is thus at a 'primitive' stage (Walters 1990) and may still be evolving.

In a review of cooperative breeding systems, Emlen (1991) identifies two logical steps necessary for their evolution. The first of these is the temporary renunciation of independent breeding (i.e. delayed reproduction), mediated by the decision to defer dispersal and thus to remain on one's natal territory. The second is the development of helping behavior once dispersal has been delayed. Alternative hypotheses concerning the evolution of delayed dispersal have been hotly debated for decades. Among those that have received the most attention is the habitat saturation hypothesis. It contends that a dearth of suitable breeding territories acts as a constraint prompting philopatry (Emlen 1991) and competition for breeding vacancies in and around the natal territory. In contrast, the benefits of philopatry hypothesis proposes that breeding sites may not be unavailable, but a marked difference in territory quality may exist such that high quality territories tend to be occupied. It further contends that it is advantageous for individuals to remain at home and compete for future vacancies in high quality territories rather than dispersing to low quality territories, where the probabilities of survival and of successful reproduction are both low (Stacey and Ligon 1987).

Habitat saturation was recently criticized as insufficient to explain delayed dispersal (Koenig et al. 1992). The same set of demographic conditions, in which the number of competitors is greater than the number of suitable territories, has been documented to lead to delayed dispersal in certain species or populations, but to alternative strategies such as floating in others (Hunter 1987). That habitat saturation does not always select for delayed dispersal is also the view of Emlen (1991, 1992), who established that the differences between the habitat saturation and benefits of philopatry hypotheses are only semantic. Both in fact rely on ecological constraints and their

concomitant costs as explanations for the development of a strategy that involves avoiding such costs. Under his general ecological constraints model, the costs arising from ecological constraints must outweigh or at least equal the cost to the reproductive component of fitness resulting from delayed reproduction. The costs associated with ecological constraints would most commonly be related to a limited availability of optimal habitat *along with* a rarity of marginal habitat. This would presumably increase the mortality risk of dispersing birds as well as lower their probability of securing a mate and of reproducing successfully (Emlen 1991). The difference in quality between habitats may be defined by limiting or critical factors. These could include a critical resource with uneven distribution among territories, or, in those species which modify their habitat, the presence or absence of the resource resulting from said modification. For the red-cockaded woodpecker, the cavity appears to be such a resource.

Cavities are extremely valuable to the red-cockaded woodpecker. The bird is non-migratory (Walters 1990, Jackson 1994) and occupies territories year-round (Walters 1990). These territories contain one or more cavity trees, which comprise what is known as the cavity tree cluster (Walters 1990). Cavities in the clusters are used by resident woodpeckers as roost sites throughout the year (Ligon 1971) and as nest sites during the breeding season (Walters 1990, Jackson 1994). Each group member roosts in its own cavity (Walters 1991, Jackson 1994). Resin flow maintained around cavities is effective in impeding the progress of predatory arboreal snakes by smoothing the climbing surface and interfering with the action of the ventral scales used by the snakes in climbing (Rudolph et al. 1990a). Cavities also provide shelter from low temperature extremes (McFarlane 1992). Cavities thus may enhance both survival (Walters et al. 1988) and reproductive output by providing protection from nest predators (Jackson 1974). The dependence of the woodpeckers on cavities suggests that cavities may qualify as a critical resource altering the quality of a territory through their presence. In an effective test of the ecological constraints hypothesis, Walters et al. (1992b; Copeyon et. al 1991) provisioned unoccupied woodpecker habitat with artificially drilled cavities and compared these sites to unoccupied control sites. Occupancy of those sites provisioned with artificial cavities was quite high, whereas none of the control sites were occupied. Walters et al. (1992b; Copeyon et. al 1991) thus succeeded in demonstrating the following: (1) that all suitable breeding habitat is not occupied; (2) that a steep gradient in quality exists between occupied and unoccupied territories; (3) that cavities represent the critical resource magnifying differences in habitat quality for the woodpecker; and (4) that the evolution of deferred natal dispersal in this species is very likely a response to ecological constraints represented by the presence or absence of cavities as indicators of habitat quality.

The absence of cavities on sub-optimal habitat appears to act as an ecological constraint to natal dispersal. However, the red-cockaded woodpecker is equipped to modify and thus to alter the quality of its habitat through the construction of cavities. The species thus has the morphological and behavioral potential to overcome this constraint. Why do the birds compete for vacancies on occupied territories with existing cavities rather than excavate cavities in unoccupied habitat ? Excavation of cavities on unoccupied habitat appears to be exceedingly rare (Walters et al. 1988), with only a few instances having been documented (Jackson 1987, Walters and Goodson 1992a and 1992b). The rate of new territory formation is extremely low and has been documented to occur primarily through territorial budding, wherein a portion of an already

existing territory is split off to become a new, independent territory with its own breeding unit (Walters et al. 1988).

Male helpers in fact attain eventual breeding status by inheriting their natal territory or by competing for breeding vacancies on neighboring territories arising through breeder mortality (Walters et al. 1988, 1992a, 1992b). This appears to be an effective strategy for acquiring breeding positions under what appear to be highly competitive conditions (Walters et al. 1992a). Walters et al. (1992b) have postulated that it is the high temporal cost involved in the process of cavity construction that makes it advantageous for individuals to compete for vacancies on already existing territories. This would make both dispersing or remaining on a natal territory preferable to excavating new cavities on unused territories. This hypothesis is supported by empirical data from two Texas populations of red-cockaded woodpeckers by Conner and Rudolph (1995a), who found excavation times in pines to vary from 1.8 to 6.3 years, depending on the species. Although these results support the hypothesis, it is questionable whether they can be extrapolated to the species as a whole. The habitat the birds occupy is marginal and the populations studied are characterized by small size and declining status. The results are also somewhat biased toward underestimating excavation and use times because these times exceeded the study period in some cases (Conner and Rudolph 1995a). Finally, estimates of both excavation and use were based on relatively small sample sizes (Conner and Rudolph 1995a). My primary objective in Part I is to quantify cavity excavation and use dynamics in three stable red-cockaded woodpecker populations in North Carolina inhabiting prime habitat (see below) in order to better evaluate the critical assumption of a high time cost of cavity excavation.

The Decline and Conservation of the Red-cockaded Woodpecker

The red-cockaded woodpecker once occupied both the Piedmont and Coastal Plain of the Southeast and ranged as far north as New Jersey, west to Texas and inland to Kentucky, Tennessee, and Missouri (Jackson 1971). This range corresponds closely to the historic range of the open, mature southern pine forests (Jackson 1971) on which the woodpecker is dependent for food and habitat (Walters 1990, Jackson 1994). These forests comprise a climax ecosystem that was once maintained by frequent fire set by lightning during the summer (Jackson et al. 1986 cited in Jackson 1994). Fire is essential to preventing the development of hardwoods (Jackson 1986), which represent the next successional stage in this system. The evolution of the bird's selection of living pine trees for cavity excavation is in fact thought to be related to the low availability of hardwoods and snags due to fire (Ligon 1970, Jackson et al. 1986 cited in Conner and Rudolph 1995a). The woodpeckers exhibit an affinity for longleaf pine (*Pinus palustris*) for roosting and nesting, but also use slash (*P. elliotii*), loblolly (*P. taeda*), shortleaf (*P. echinata*), pitch (*P. rigida*) and pond (*P. serotina*) pines (Jackson 1971). In the past century, decimation of the longleaf pine ecosystem on which it depended has led to the virtual extirpation of the woodpecker north of North Carolina and in all interior states except Arkansas (Walters 1990). The woodpecker now generally occurs in small, fragmented populations (USFWS 1985).

Most responsible for loss of the woodpecker's habitat was the rise of the timber and naval stores industries of the 18th century, which by 1930 had depleted virtually all virgin forest in the South (Ware et al. 1993). The woodpeckers have a well-documented preference for old growth

for the excavation of cavities (Jackson and Jackson 1986, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988, Rudolph and Conner 1991). Selected trees generally average at least 80-120 years of age (Jackson et al. 1979, USFWS 1985), but much older trees are used when they are available (Rudolph and Conner 1991). This is connected to the need for a sufficient amount of heartwood to contain a cavity (Walters 1990) and to the tendency of pines to become infected by red heart fungus (*Phellinus pini*) at an older age (Walters 1990, Conner 1995). Decay of the heartwood caused by the fungus is believed to reduce the time required for excavation. There is also evidence that older trees are preferred for foraging (Zwicker 1995). Logging into the 20th century has been characterized by short rotations (Jackson 1986), which results in the harvesting of trees before they are of an age suitable for cavity excavation. It has also led to the replacement of longleaf pine, which is most commonly used by the woodpecker, with faster-growing species such as loblolly and slash pine. The advent of the era of modern fire suppression provided an additional obstacle to the regeneration of old-growth, as invasion of fire-suppressed areas by shrubs and hardwoods prevented pine reproduction (Ware et al. 1993). In addition, growth of hardwood midstory to cavity level forces the woodpeckers to abandon their cavities (Locke et al. 1983, Hovis and Labisky 1985, Conner and Rudolph 1991, Loeb et al. 1992), as their ability to protect the cavities against predation is compromised.

All of these factors have severely impacted the woodpecker's ability to survive and reproduce (USFWS 1985). Currently, the woodpeckers are dependent on a small pool of remaining old growth trees which is subject to steady decline through tree mortality. In many areas, second growth pine will not reach the age at which it will be suitable for cavity excavation for 20-40 year (Costa and Escano 1989).

Many of the remaining woodpecker populations occur on state lands and on federal lands (Jackson 1971) such as military installations and national forests. Conservation efforts on public lands originally focused on the protection of existing cavity trees and on the preservation of buffer zones around them (Hooper 1995). The recent development of new management tools such as the artificial cavity (Copeyon 1990), the cavity insert (Allen 1991) and the cavity restrictor (Carter et al. 1989), in conjunction with a better understanding of population dynamics (Walters et al. 1988), have led to the development of new management strategies which make the outlook for recovery more promising. Because of its cooperative breeding system, reproductive output in the species is a function of the number of woodpecker groups in the population, rather than of the number of individual woodpeckers. It is now understood that the number of groups in a population is directly linked to the number of clusters with suitable cavities (Walters 1991). Management efforts are thus increasingly focused toward retaining existing clusters and promoting population expansion through the creation of new ones. Such efforts include the direct management of clusters through hardwood removal and prescribed burns, the construction of artificial cavities for supplementation of existing clusters and creation of new clusters, as well as the translocation of birds (Conner et al., unpublished). These management techniques are all part of short-term recovery efforts that can contribute to reversing declines and even bring about increases in populations of the woodpecker. As second growth trees mature and populations are stabilized, it is hoped that long-term recovery plans focusing on ecosystem management of mature pine forests will take their place (Conner et al., unpublished). In the meantime, implementation of these management techniques over the next few decades will be critical for the recovery of the

species. Continuous monitoring of cavity populations during this period is imperative. As part of the second objective of Part I of this thesis, patterns of gains and losses of four cavity populations in North Carolina are quantified for the period of nine to sixteen years over which the populations have been monitored. Losses and gains are further examined in relation to their underlying causes, and management recommendations are made based on the current status of each cavity population.

Chapter 2: Methods

Study Area

The data employed in these analyses were collected as part of ongoing studies of the red-cockaded woodpecker in North Carolina. Two distinct woodpecker populations, on Camp LeJeune Marine Base (CL) and on the Croatan National Forest (CNF), are both located in the Coastal Plain of eastern North Carolina. The former encompasses 34,615 ha and the latter 63,907 ha. An additional population is found on the Fort Bragg Military Reservation and in and around the towns of Southern Pines, in the Sandhills region of south-central North Carolina. Sampling of the population took place on the western third of Fort Bragg (FB), which consists of approximately 12,000 ha, and on Camp Mackall (MACK), which consists of nearly 2,830 ha. All populations are completely marked. Although the woodpeckers on FB and MACK are part of one large population, the cavity populations on these two study areas were treated in this thesis as distinct from one another.

The plant communities on FB and MACK are similar, though they occur in different proportions in the two study areas. The majority of habitat consists of two types of pine savanna, pine-scrub oak sandhill and xeric sandhill scrub (Carter, pers. comm.), which are characterized by second-growth with scattered old-growth trees (Walters et al. 1988). The remaining habitat is comprised of mesic pine flatwoods and three wetland communities: streamhead pocosin, Coastal Plain small stream swamp blackwater subtype (mostly hardwoods), and sandhill seep. Although some red-cockaded woodpeckers nest and roost in pond pines in the pocosins, the majority are concentrated in longleaf pines in the savannas (Carter, pers. comm.).

CNF is characterized primarily by pocosin wetlands, mesic and wet pine flatwoods and pine-scrub oak communities (Christensen 1988). Red-cockaded woodpeckers are concentrated in the flatwoods and pine-scrub oak communities, but occur in pond pines in pocosins as well (Walters et al. 1995a). The forested areas on CL consist mainly of high pocosin wetlands, pond pine woodlands, pine savannas, and wet and mesic pine flatwoods (Schafale and Weakley 1990). More than one half of the natural areas are comprised of pure pine stands, approximately one quarter are mixed-pine hardwood forest, and one fifth are pure hardwoods. A relatively small area is wooded wetland (Camp LeJeune 1987 cited in Zwicker 1995). Old trees that were missed or rejected by loggers at the beginning of the century are scattered over the entire base (Zwicker 1995). In this study area, red-cockaded woodpeckers are largely associated with pure longleaf stands, but are also found in older mixed stands (Camp LeJeune 1987 cited in Zwicker 1995).

Data Collection

The data used in the analyses were collected from 1980-1995 on FB and MACK, from 1986-1996 on CL and from 1988-1996 on CNF. Information on status of cavities was updated once yearly during the woodpecker's breeding season of these years between March 1 and June 30. Updates provide data on various physical characteristics of cavities as well as on the health and condition of cavity trees. The data are used to monitor progress in cavity excavation and use over the years. In addition, nest checks were conducted during the breeding season of each year as

part of population monitoring procedures as outlined in Walters et al. (1988). Nest checks yield information on the identity of the nest cavity in each cluster. Barring re-nesting following nest failure, only one nest cavity exists per cluster per breeding season.

Six cavity and tree variables from the updates, as well as nest information, were used to determine cavity status in this thesis. All six specifically impact the interpretation of whether a completed cavity is actively used and whether a non-completed cavity is actively excavated. They are: (1) stage of cavity excavation, (2) activity status of a cavity, (3) degree of healing of a cavity, (4) degree of cavity enlargement, (5) status of a cavity tree as living or dead, and (6) status of a cavity as broken or not broken from a cavity tree. These variables are described in detail below.

Cavity excavation (1) is a gradual process, yet it is possible to categorize excavation into distinct stages. The first three of these, *substarts*, *starts* and *advanced starts*, are stages of non-completed cavities. Substarts consist of a shallow break into the sapwood, which is living xylem tissue. Excavation at this stage typically results in copious oleoresin (pine gum or sap) flow from the wound, which serves to deter insects from infesting the tree (Stern 1988, Conner and Rudolph 1995a). Sap is a combination of turpentine, a liquid solvent, and rosin, a waxy substance (Stern 1988). The turpentine evaporates once out in the air, and the layer of rosin that is left behind prevents water loss and fungal attacks (Stern 1988). Sap flow can interfere with cavity excavation, and it is not until the sap hardens after saturating the wood around the wound through the process of resinosis that excavation can resume (Conner and Rudolph 1995a). Starts are less than 10 cm deep and represent the initial excavation of the entrance tunnel through living sapwood. Again, resin production results in resinosis at this stage. Advanced starts are at least 10 cm deep and often extend beyond the sapwood and into the heartwood, which consists of dead xylem tissue (Stern 1988). Once into the heartwood, where sap flow can no longer affect excavation, initial construction of the cavity chamber begins (Conner and Rudolph 1995a). Construction of resin wells, which are small puncture wounds exposing the sapwood around the circumference of the tree above cavity height, may begin at this stage, and intensifies as the cavity nears completion. Maintenance of resin wells results in active sap flow around a cavity, creating a barrier of sap effective against predators such as snakes (Rudolph et al. 1990a). It is often during construction of advanced starts that woodpeckers will begin to roost in a cavity tree (Conner and Rudolph 1995a). Excavation proceeds on the cavity chamber until the chamber is finished. It is at this point that the cavity is regarded as *completed*. Characteristic of completed cavities is development around the cavity entrance of a 'plate', an area of cambium contiguous with the cavity opening exposed through the chipping away of bark by the woodpeckers. Plates may be found around non-completed cavities, although this is rare. Cavities are sometimes judged during updates to have been completed just shortly before a cavity is updated. These cavities are referred to as *recently completed* cavities, and are characterized by the presence of few resin wells and by the beginnings of a plate. Shallow breaks into the sapwood that may not have been excavated by red-cockaded woodpeckers are recorded as *possible starts*, and cavities whose status could not be determined as *'unknown'*.

A qualitative measure of the activity associated with a cavity is recorded during field updates. The activity status (2) of non-completed cavities denotes whether they have been recently excavated. The activity status of completed cavities denotes whether they are being used for

roosting by red-cockaded woodpeckers. Designation of activity status is determined by the physical characteristics of a cavity. The color of the cavity interior is diagnostic in non-completed cavities: bright yellow wood signifies recent excavation activity, while grayish or dark yellows indicate inactivity. The presence of wood particles in the entrance tunnel, of fresh chipping (excavation lending the bark a characteristic reddish color) around the rim of the cavity, and of fresh sap are also standard indicators of recent excavation activity. In completed cavities, activity is denoted by the presence of red chipping in and around the cavity and of fresh sap exuding from resin wells. Active resin wells especially are accurate indicators of use of cavities by red-cockaded woodpeckers (Jackson 1977a).

Based on these and other characteristics, cavities are categorized as *active*, *inactive*, and, in ambiguous cases, as *possibly active*. Both completed and non-completed cavities that have been abandoned by red-cockaded woodpeckers for several years are recorded as *relict* cavities when they develop certain physical characteristics. For completed cavities, these include healing of the resin wells and of the plate. For both completed and non-completed cavities, they also include the absence of fresh chipping and of fresh sap, or the presence of old, dried, dirty gray to brownish-colored sap. Often the cambium will also have healed over the cavity opening, although this is more commonly associated with non-completed cavities. Healing over of the cavity (3) in this manner is categorized into *partial* and *complete* healing. The former category encompasses a wide range, from slight healing to almost complete healing. In the analyses, completely healed cavities were considered to be inaccessible and thus unusable to the woodpeckers, whereas partially healed cavities were not.

Enlargement of cavities (4) by other woodpecker species (Carter et al. 1989), notably red-bellied woodpeckers (*Melanerpes carolinus*), red-headed woodpeckers (*M. erythrocephalus*), pileated woodpeckers (*Dryocopus pileatus*) and northern flickers (*Colaptes auratus*), has the potential to affect use of completed cavities and excavation of non-completed cavities. Enlargement of a cavity often leads to cavity abandonment (Carter et al. 1989), presumably because the cavity is usurped by other species or harder to defend (McFarlane 1992). Like healing and excavation, degree of enlargement is a continuum, but three distinct, qualitative measures of degree of enlargement have been identified. Each category can be used to refer to either the cavity entrance or the cavity chamber, so that either structure may be *slightly*, *moderately* or *greatly* enlarged.

Tree death (5) renders cavities undesirable to red-cockaded woodpeckers, presumably because of the dead tree's inability to produce fresh sap (Wayne 1906 cited in Ligon 1970, McFarlane 1992), making the cavity more accessible to snakes (Jackson 1974, Rudolph et al. 1990a), and potentially because of a dead tree's susceptibility to fire (Ligon 1970). Trees are killed by a variety of agents, including disease, lightning strikes, beetle infestations, fire and wind. Although pine trees are highly-fire resistant, ignition of the highly-flammable sap flowing from the resin wells can result in damage to the tree leading to death (Conner and Locke 1979). Wind can kill a tree by blowing it over and exposing the roots or by causing the tree to break at the cavity (Conner et al. 1991, Conner and Rudolph 1995b). The physical loss of a cavity from a tree (6) can also occur in the latter manner without killing the tree.

Not all cavities were updated consistently in the breeding season of each year, so that gaps in the data exist in relation to the variables discussed above. Because the analyses rely on consistency in data collection, a protocol was developed to infer the missing measure of each variable where possible (see Appendix).

Data Analysis: Survival Analysis

A majority of the analyses dealing with estimation of duration of cavity excavation and of cavity use were accomplished using survival analysis (Forthofer and Lee 1995, Parmar and Machin 1995). This statistical technique is commonly employed in the estimation of survival time, which is measured as the length of time between an initial state or event (e.g., commencement of excavation) and a subsequent state or event of interest (e.g., completion of excavation or permanent suspension of cavity use) (Parmar and Machin 1995). Survival time can not be calculated directly when the subsequent event has not been observed prior to the time at which data collection ceases (Forthofer and Lee 1995). For these incomplete observations, survival time is said to be censored (Forthofer and Lee 1995, Parmar and Machin 1995), or, more specifically, right-censored (Turnbull 1974). Thus, a cavity upon which excavation has not been completed by the last year of data collection is said to represent a right-censored observation, as is a cavity that is still being actively used. Similarly, if the initial event (initial excavation or use) occurred prior to commencement of the study, the resulting survival time is left-censored (Turnbull 1974). Omission of censored observations from an analysis results in a reduction in sample size and potentially introduces a selection bias in the results (Forthofer and Lee 1995), as observations associated with survival times that are longer than the study are excluded. By incorporating censored data into the analyses, survival analysis produces results that are more accurate. The data collected here tend to be simultaneously right- and left-censored. While well developed methodology exists for dealing with either right- or left-censored data separately, statistical techniques for handling doubly-censored data are fairly recent, not well established and generally still under development. Because of this, the analyses were conducted on right-censored data alone.

Survival analysis makes use of either of two methods in order to estimate survival curves. The life-table method is based on the concept of the population life table and groups subjects into (generally yearly) survival intervals from the time sampling on each subject begins (Forthofer and Lee 1995). Grouping is independent of the fate of each subject (i.e. when the event of interest is observed). The Kaplan-Meier, or product-limit, method is a non-parametric technique that is instead based on the actual survival time for each subject, and subjects are grouped according to survival time (Forthofer and Lee 1995). Both methods yield similar results. The life-table method is normally employed for large data sets (Forthofer and Lee 1995), while the Kaplan-Meier method is used for data sets with sample sizes below or around 100 (Forthofer and Lee 1995). Given the sample sizes available for my analyses, as well as the flexibility inherent in using a statistical tool that makes no assumption about the distribution of the data involved, the Kaplan-Meier method was used exclusively.

Statistica (1993) was used to generate a series of cumulative survival probabilities according to the Kaplan-Meier method, which is described in Forthofer and Lee (1995). A mean value was in

turn calculated from the survival probabilities using methodology described in Forthofer and Lee (1995). Statistica (1993) was also used to generate median values, which are defined as the length of time corresponding to a cumulative survival probability of 0.5 (Forthofer and Lee 1995). For the analysis of duration of excavation, for example, the median is thus defined as the length of the excavation period corresponding to the point at which 50 % of non-completed cavities have reached the next stage of excavation. Median values are reported preferentially over means in survival analyses, as the distributions of survival time data are often skewed to the right due to a smaller number of longer-term 'survivors' (Parmar and Machin 1995).

As the proportion of censored data affects the calculation of cumulative probabilities of survival, large proportions may result in the inability to estimate median survival times. In these cases, the first quartile, or 25th percentile, was reported in the place of the median. Furthermore, if the longest survival time in a sample is censored, the resulting mean survival time will be an underestimate of the true mean, as it will be restricted to the time frame of the study (Forthofer and Lee 1995). The restricted means were calculated not as restricted to the highest observed value, or maximum value, reported in the tables (see below), but as restricted to the highest uncensored value. While both methods of calculating restricted means are legitimate (Forthofer and Lee 1995, Klein and Moeschberger 1997), basing means on the highest censored value would lead to higher estimates. As high censored values often represent outliers, basing the means on the highest uncensored value reduces the probability of skewing the means. Calculation of the median value is not affected by choice of method, however. For each of the analyses employing survival analysis, minimum and maximum values were reported in place of standard deviations because equations for measuring variance in the sample were not available. As an additional substitute, the percentage distribution of duration in years of cavity excavation and use are reported graphically.

In survival analysis, subjects whose status can not be assessed at the closing date of the study are included in the analyses as lost-to-follow-up (Forthofer and Lee 1995). Cavities that are lost-to-follow-up are cavities that were not updated for one or more consecutive years including the last year of the study. These cavities were considered censored in the year in which they were last updated (Forthofer and Lee 1995).

In addition to the calculation of means and medians, survival curves were compared between the tree species in which the cavities were excavated, as differences between them may contribute to preferential excavation and use of certain species. Curves were also compared between cavity populations in order to assess the significance of differences between them in duration of cavity excavation and use. Because samples sizes for MACK generally were small, data for MACK and for FB were analyzed together. Comparisons were executed using the non-parametric Gehan's generalized Wilcoxon test for two curves and an extension of this test for three curves.

Chapter 3: Dynamics of Cavity Excavation

Methods

Timing of Excavation

Excavation of cavities by red-cockaded woodpeckers is a seasonal activity. Although it may begin during the breeding season, excavation normally peaks in the summer months of the post-breeding season period and ceases before winter (Walters, pers. comm.). Cavity updates that are conducted during the breeding season thus reflect the results of the excavation effort of the previous year. Although the analysis of duration of excavation is based on breeding season updates, the calculation of the absolute values of excavation length are not affected, except in the following cases. Duration of excavation is underestimated in those cases in which excavation of a cavity to a particular stage occurs during the breeding season of a given year, rather than during the post-breeding season of the previous year. Underestimation may also occur if data were collected following, rather than during, the breeding season of a particular year in which the completion of a new stage was recorded. In these cases it is unclear whether a cavity was excavated to the new stage during the post-breeding season of the year in which it was first recorded at that stage, or during the post-breeding season of the previous year. In such cases I assumed the latter was true, which may have resulted in the underestimation of duration of excavation in some cases.

Description of Analyses

Mean and median duration (measured in years) of cavity excavation by red-cockaded woodpeckers were calculated based on data collected during the breeding season of each year from each of the cavity populations. Estimation of duration of excavation included three sets of analyses. The first, duration of excavation for the entire excavation process, employed only successfully completed cavities for which excavation was observed from the substart stage (or start stage; see next section) to cavity completion. Although it did not make use of all available data, this analysis is useful in providing baseline results against which to compare the other analyses. The second set of analyses estimated duration of excavation for each stage transition (substart to start, start to advanced start, advanced start to completed cavity) using only those cavities for which excavation to the next stage was successfully completed. Using this method, certain cavities may have been used in the calculation of duration of more than one stage transition. The sum of the excavation periods calculated for each stage transition is representative of the duration of the entire excavation process. The final set of analyses likewise resulted in separate estimates for each stage transition and in a sum total of these estimates. However, this set of analyses employed survival analysis in order to make use of additional cavities for which excavation to the next stage was not completed.

The advantage of quantifying excavation as the sum of its component stages is that it has the potential to yield more accurate estimates. Because each study period is limited to a certain number of years, the entire excavation process from start to finish will have been recorded for relatively few cavities. These cavities will likely have been those with unusually short excavation

times, so that the resulting estimates of excavation duration will be biased. Estimates based on quantification of the excavation period for each stage transition, however, are bound to be more accurate, because the period is relatively short for each of the transitions and will thus have been empirically measured for a relatively large number of cavities.

Criteria for Inclusion of Data into Analyses

In order that the inclusion of left-censored data be avoided, the analyses included only those cavities for which the year of completion of the initial stage in a transition was recorded. If completion of the next stage in a transition occurred, only cavities for which the year of completion was determined were included. The exception are those non-completed cavities for which data collection ceased prior the end of a study. These cavities were included as lost-to-follow-up.

The year of completion of the relevant stages was inferred in certain cases in which it was not unequivocally known. Excavation of substarts was assumed to have been initiated in the year in which data for the substart were first collected. This assumption will have led to an underestimation of excavation periods for substarts on which excavation began prior to their first recorded appearance in the data sets. For starts that were on trees with other cavities that were updated in the preceding year, but for which a substart stage was not recorded, excavation was assumed to have been initiated in the year in which data on the starts were first collected. This assumption is reasonable given that the transition from substart to start is believed to be rather short (Walters, pers. comm.). The assumption may have resulted in the underestimation of excavation periods for those starts that were overlooked during field updates in years previous to their first being recorded.

Sometimes entrance tunnels are excavated so that they become connected with an existing cavity chamber, resulting in what are referred to as common cavities. Because creation of a common cavity does not involve excavation of a new cavity chamber, advanced starts that became common cavities upon completion were not included in the analyses. Such starts were included, however, if they became common cavities following the year of completion, as in this case a new cavity chamber was excavated (see Appendix).

Because duration of excavation was measured as a natural process, those cavities subject to management activities were not included in the analyses, as such activities may affect duration of excavation. Excluded were cavities that were drilled as advanced starts, regardless of whether they were subsequently completed by the woodpeckers. Excluded also were non-completed cavities fitted with cavity restrictors. Restrictors are metal plates placed around a cavity entrance (Carter et al. 1989). They are designed to prevent cavity enlargement, or access leading to usurpation of already enlarged cavities, by species larger than the red-cockaded woodpecker (Carter et al. 1989).

Survival Analysis

In estimating duration of excavation through survival analysis, a set of criteria was established to discriminate between those observations for which the possibility of future excavation exists versus those for which it is highly unlikely or nil. Observations falling into the latter category were not included in the analyses. Excluded were those non-completed cavities that healed over completely, those on a section of trunk that broke from the rest of the tree, those that were on a tree that died, or those that were otherwise damaged such that excavation could no longer progress. This occurred through damage by pileated woodpeckers or by a cavity becoming clogged with free-flowing sap. Also excluded were those non-completed cavities that attained relict status, as reactivation of relict cavities is rare. Reactivated relicts were included in the analyses, unless they subsequently reverted to relict status or were subjected to any of the events listed above. Non-completed cavities enlarged by other woodpecker species were not excluded as it was not clear that enlargement acted as a deterrent to further excavation. Non-completed cavities in clusters that were intermittently abandoned were also included because cluster abandonment is a natural factor influencing duration of excavation.

Variable percentages of the non-completed cavities meeting the above criteria were inactive for one or more consecutive years up to and including the last year of a study, suggesting that they had not been excavated during this period. A non-completed cavity that is abandoned by red-cockaded woodpeckers may require several years to develop those physical characteristics that identify it as a relict and disqualify it from the analyses. It was therefore necessary to determine the probability of inactive cavities being excavated again, or reactivated, based on the length of time they were inactive. This was accomplished by calculating a series of reactivation rates based on the concept of the hazard rate. In survival analysis, a hazard rate corresponds to the proportion of subjects dying in an interval per unit time (Forthofer and Lee 1995). As used in this particular analysis, a reactivation rate is defined as the proportion of non-completed cavities that progress to the next stage of excavation or upon which excavation resumes following a period of inactivity of a given number of consecutive years. Reactivation rates were calculated separately for each of the three stage transitions and for each of the pine species in which cavities are excavated using methods described by Parmar and Machin (1995) (Tables 3.1 and 3.2). Based on these reactivation probabilities, the appropriate proportion of cavities that had been inactive for each number of years was randomly excluded (i.e. it was assumed these cavities would be lost or become relicts, and thus never be completed) and the remainder were included as censored observations.

Included in the calculation of reactivation rates were (1) those cavities for which the breeding season marking the beginning of an inactive period was known and (2) those cavities that were updated consistently during the breeding seasons for the entire length of the inactive period. The length of inactive periods was based exclusively on breeding season records: cavities inactive during the breeding season but active outside of the breeding season were regarded as inactive. If a cavity underwent more than one distinct period of inactivity, only the first period meeting the above requirements was incorporated into the calculations. All cavities meeting these requirements were used in the calculations regardless of fate, enlargement status, or of whether

their cluster had resident birds. Relict cavities were also included and regarded as inactive cavities in the calculations. Advanced starts becoming common with other cavities were not included.

The field protocol for FB and MACK was such that cavity information pertaining to inactive, non-completed cavities was recorded during updates only as time permitted. In order to bridge gaps in these data for the calculation of reactivation rates, the assumption was made that non-completed cavities on FB and MACK that are missing records in certain years were (1) updated during the breeding season of those years, (2) found to be inactive and (3) found not to have progressed to a new stage of excavation since the previous year. Although this assumption will have resulted in the potential overestimation of periods of inactivity for the few cavities that were not monitored during certain years, it eliminated the bias toward cavities showing signs of activity. The percentage of cavities for which the assumption was used was 35.5 % for FB and MACK.

Results

Red-cockaded woodpeckers in the study populations excavated cavities in longleaf, loblolly and pond pine. Because survival analysis requires at least four uncensored observations in order to yield reliable parameter estimates (Statistica 1993), calculation of duration of excavation for pond pine was not possible due to small sample sizes. Small sample sizes also were problematic in calculating reactivation rates for substarts in longleaf and loblolly. Therefore, I employed the following procedures. For both longleaf and loblolly pine, calculation of reactivation rates for substarts on CNF and CL employed data from both longleaf and loblolly pine (Tables 3.1 and 3.2). For CL, these rates also included data from CNF. Reactivation rates for substarts on FB/MACK could not be calculated at all.

More than 70 % of the non-completed cavities followed in each of the cavity populations were not excavated to completion by the end of each study (Table 3.3). Approximately 20-30 % of these were abandoned by the woodpeckers and approximately 10 % were lost (i.e. were on trees that died or broke from trees) before they could be completed. More cavities were completed (~ 30.0 %) and fewer abandoned on CL than in the other populations, where approximately 20 % of the cavities followed were excavated to completion.

Duration of the Entire Excavation Process

Comparison of Analyses

Estimated means and medians were generally comparable to one another within each analysis for all cavity populations. When they differed, mean values generally were higher than medians. Because medians are reported preferentially over means in survival analysis, the comparisons that follow are based on median values.

Median estimates of the duration of the entire excavation process varied between analyses and between cavity populations, but were consistently two years or greater in loblolly and three years

TABLE 3.1. Reactivation rates of cavities excavated in longleaf pine following periods of continuous inactivity of varying lengths.

Cavity population	<i>Substart</i>			<i>Start</i>		<i>Advanced Start</i>	
	No. years inactive	Sample size	Reactivation rate	Sample size	Reactivation rate	Sample size	Reactivation rate
<i>FB/MACK</i>	1	51	0.235	438	0.267	165	0.321
	2	36	0.083	263	0.198	88	0.284
	3	29	0.069	170	0.141	53	0.264
	4	23	0.087	126	0.087	31	0.258
	5	19	0.000	107	0.103	20	0.050
	6	15	0.000	89	0.090	19	0.158
	7	14	0.071	71	0.042	15	0.133
	8	13	0.000	58	0.052	11	0.000
	9	11	0.091	43	0.023	8	0.125
	10	10	0.000	32	0.000	4	0.000
	11	4	0.000	28	0.000	3	0.000
	12	3	0.000	16	0.063	1	0.000
	13	1	0.000	7	0.000	0	--
	14	1	0.000	0	--	0	--
	15	1	0.000	0	--	0	--
<i>CNF</i>	1	21	0.143	107	0.206	61	0.492
	2	11	0.000	73	0.110	24	0.208
	3	8	0.000	59	0.051	14	0.214
	4	3	0.000	50	0.020	9	0.000
	5	3	0.000	37	0.054	7	0.000
	6	2	0.000	21	0.000	5	0.167
	7	2	0.000	16	0.000	5	0.000
	8	0	--	1	0.000	0	--
<i>CL</i>	1	26	0.154	54	0.315	31	0.387
	2	11	0.000	32	0.250	16	0.125
	3	8	0.000	21	0.190	11	0.000
	4	3	0.000	14	0.071	11	0.364
	5	3	0.000	12	0.083	4	0.000
	6	2	0.000	6	0.000	3	0.333
	7	2	0.000	3	0.333	2	0.000
	8	0	--	1	0.000	2	0.000
	9	0	--	0	--	2	0.000

TABLE 3.2. Reactivation rates of cavities excavated in loblolly pine following periods of continuous inactivity of varying lengths.

Cavity population	<i>Substart</i>			<i>Start</i>		<i>Advanced Start</i>	
	No. years inactive	Sample size	Reactivation rate	Sample size	Reactivation rate	Sample size	Reactivation rate
<i>FB/MACK</i>	1	--	--	28	0.250	17	0.235
	2	--	--	18	0.111	9	0.222
	3	--	--	12	0.000	6	0.000
	4	--	--	8	0.000	4	0.000
	5	--	--	7	0.000	4	0.000
	6	--	--	7	0.143	4	0.000
	7	--	--	5	0.000	4	0.000
	8	--	--	4	0.000	2	0.000
	9	--	--	3	0.000	2	0.000
	10	--	--	2	0.000	2	0.000
	11	--	--	1	0.000	2	0.000
	12	--	--	0	--	2	0.000
	13	--	--	0	--	2	0.000
	14	--	--	0	--	1	0.000
<i>CNF</i>	1	21	0.143	38	0.132	15	0.400
	2	11	0.000	29	0.207	7	0.143
	3	8	0.000	19	0.000	4	0.000
	4	3	0.000	18	0.111	2	0.000
	5	3	0.000	13	0.000	1	0.000
	6	2	0.000	8	0.000	1	0.000
	7	2	0.000	6	0.000	0	--
<i>CL</i>	1	26	0.154	15	0.533	26	0.385
	2	11	0.000	6	0.167	10	0.500
	3	8	0.000	4	0.000	4	0.500
	4	3	0.000	2	0.500	2	0.500
	5	3	0.000	2	0.500	1	0.000
	6	2	0.000	0	--	0	--
	7	2	0.000	0	--	0	--

TABLE 3.3. Fate of cavities of non-completed status at the start of and throughout each study on *FB/MACK*, *CNF* and *CL*. Completed category represents cavities that were completed by the end of a study. Lost category represents cavities that were on trees that died, cavities that snapped from their tree, cavities that suffered extensive pileated woodpecker damage and cavities for which sap production prohibited further excavation. Not completed category represents cavities that were not completed by the end of a study. Abandoned category represents cavities in clusters with no resident birds in the last year of a study. Unknown fate category represents cavities that were not updated in the last year of a study.

Cavity population	Completed	Healed or relict	Lost	Not completed	Abandoned	Unknown fate
<i>CL</i>	29.5	19.5	12.4	36.6	0.0	2.0
<i>CNF</i>	18.8	33.6	7.4	37.4	1.0	1.8
<i>FB/MACK</i>	20.1	31.1	8.7	37.7	2.2	0.2

or greater in longleaf pine (Tables 3.4-3.6). Within each cavity population, the shortest estimates resulted from the analyses using only successfully completed cavities (longleaf median = 3.0 to 5.0, loblolly median = 2.0 to 5.5) and only successfully completed stages (longleaf median = 4.0 to 6.0, loblolly median = 4.0 to 5.5), although the latter tended to be higher. Estimates obtained from the analysis that included censored observations were two to three times as large for longleaf (median = 9.4 to 13.1) and 1.5 to five times as large for loblolly pine (median = 4.0 to 10.0). Duration of excavation for the FB/MACK population is underestimated for loblolly because the length of the transition from substart to start could not be calculated.

Based on these results, it is clear that the methodology used in the quantification of duration of cavity excavation has a profound effect on the outcome of the analyses, and that selectivity in the data used can lead to results that are inaccurate and biased toward underestimation.

TABLE 3.4. Duration in years of cavity excavation from substart/start to completed cavity by the red-cockaded woodpecker. Includes only successfully completed cavities. Maximum duration that could have been observed during a study was 14 years for FB/MACK, 8 years for CNF and 10 years for CL.

Cavity population	Species	n	Median	Mean	SD	Min.	Max.
FB/MACK	Longleaf	38	5.0	5.4	2.7	2.0	12.0
	Loblolly	2	5.5	5.5	3.5	3.0	8.0
CNF	Longleaf	8	3.0	4.1	1.6	3.0	7.0
	Loblolly	7	4.0	3.9	1.2	2.0	5.0
CL	Longleaf	13	3.0	3.7	1.9	2.0	8.0
	Loblolly	2	2.0	2.0	0.0	2.0	2.0

TABLE 3.5. Duration in years of cavity excavation, divided into its component stages, by the red-cockaded woodpecker, for the analyses of uncensored observations.

Cavity population	Stage transition	Species	n	Median	Mean	SD	Min.	Max.
<i>FB/MACK</i>	Substart to Start	Longleaf	43	1.0	1.5	1.1	1.0	7.0
		Loblolly	1	1.0	1.0	0.0	1.0	1.0
	Start to Advanced start	Longleaf	47	3.0	3.6	2.5	1.0	13.0
		Loblolly	4	1.0	1.3	0.5	1.0	2.0
	Advanced start to Cavity	Longleaf	110	2.0	2.3	1.6	1.0	8.0
		Loblolly	9	2.0	1.8	0.8	1.0	3.0
	Sum of stages	Longleaf		<i>6.0</i>	<i>7.4</i>	<i>5.2</i>		
		Loblolly		<i>4.0</i>	<i>4.1</i>	<i>1.3</i>		
<i>CNF</i>	Substart to Start	Longleaf	14	1.0	1.5	1.1	1.0	4.0
		Loblolly	4	1.0	1.3	0.5	1.0	2.0
	Start to Advanced start	Longleaf	13	2.0	2.6	1.9	1.0	6.0
		Loblolly	5	2.0	2.0	1.2	1.0	4.0
	Advanced start to Cavity	Longleaf	34	1.0	2.4	1.7	1.0	6.0
		Loblolly	8	1.0	1.3	0.5	1.0	2.0
	Sum of stages	Longleaf		<i>4.0</i>	<i>6.5</i>	<i>4.7</i>		
		Loblolly		<i>4.0</i>	<i>4.6</i>	<i>2.2</i>		
<i>CL</i>	Substart to Start	Longleaf	11	1.0	1.6	0.8	1.0	3.0
		Loblolly	4	1.0	1.3	0.5	1.0	2.0
	Start to Advanced start	Longleaf	19	2.0	2.4	1.6	1.0	7.0
		Loblolly	4	3.5	3.5	2.4	1.0	6.0
	Advanced start to Cavity	Longleaf	21	1.0	2.5	2.6	1.0	11.0
		Loblolly	12	1.0	1.4	0.8	1.0	3.0
	Sum of stages	Longleaf		<i>4.0</i>	<i>6.5</i>	<i>5.0</i>		
		Loblolly		<i>5.5</i>	<i>6.2</i>	<i>3.7</i>		

TABLE 3.6. Duration in years of cavity excavation, divided into its component stages, by the red-cockaded woodpecker, for the survival analyses.

Cavity population	Stage transition	Species	n	% censored obs.	Median	Mean	Min.	Max.	
<i>FB/MACK</i>	Substart to Start	Longleaf	58	25.9	1.0	2.2	1.0	7.0	
		Loblolly	2	50.0	--	--	1.0	4.0	
	Start to Advanced start	Longleaf	159	70.4	9.1	8.4*	1.0	15.0	
		Loblolly	8	50.0	2.0	1.6*	1.0	11.0	
	Advanced start to Cavity	Longleaf	199	44.7	3.0	4.4*	1.0	15.0	
		Loblolly	16	43.8	2.0	2.3*	1.0	15.0	
	Sum of stages	Longleaf				<i>13.1</i>	<i>15.0*</i>		
		Loblolly				<i>4.0**</i>	<i>3.9**</i>		
<i>CNF</i>	Substart to Start	Longleaf	26	46.2	1.7	1.6*	1.0	4.0	
		Loblolly	7	42.9	1.4	1.6*	1.0	3.0	
	Start to Advanced start	Longleaf	38	65.8	4.0	4.2*	1.0	7.0	
		Loblolly	16	68.8	3.1	3.3*	1.0	6.0	
	Advanced start to Cavity	Longleaf	72	51.4	4.0	4.0*	1.0	8.0	
		Loblolly	17	52.9	2.0	1.6*	1.0	7.0	
	Sum of stages	Longleaf				<i>9.7</i>	<i>9.8*</i>		
		Loblolly				<i>6.5</i>	<i>6.5*</i>		
<i>CL</i>	Substart to Start	Longleaf	14	21.4	1.8	1.9*	1.0	4.0	
		Loblolly	5	20.0	1.0	1.4	1.0	2.0	
	Start to Advanced start	Longleaf	31	38.7	3.0	3.5*	1.0	9.0	
		Loblolly	16	75.0	6.0	5.1*	1.0	9.0	
	Advanced start to Cavity	Longleaf	49	59.2	4.6	4.4*	1.0	10.0	
		Loblolly	28	57.1	3.0	2.3*	1.0	9.0	
	Sum of stages	Longleaf				<i>9.4</i>	<i>9.8*</i>		
		Loblolly				<i>10.0</i>	<i>8.8*</i>		

* Restricted mean (see Chapter 2)

** Does not include substart to start.

Comparison of Pine Species

Meaningful tests of significance could not be performed when estimated excavation time was based on the sum of the estimates of duration of each stage transition. Inferences were instead made based on statistical comparisons of each stage transition: if no significant differences exist between species for all of the transitions, then the resulting sums are also not likely not to be significantly different.

Median estimates within each cavity population were comparable between species in the analyses using only successfully completed cavities (Table 3.4) and only successfully completed stages (Table 3.5). Differences were not statistically significant in the former analysis (Mann-Whitney U test, $U = 36.0$, $p = 0.900$ (FB/MACK); $U = 65.5$, $p = 0.853$ (CNF); $U = 113.0$, $p = 0.110$ (CL)), but were highly significant in the latter analysis for the start to advanced start stage transition for one of the cavity populations, FB/MACK (Table 3.7). The estimate of the duration of the entire excavation process for FB/MACK is of 6.0 years for longleaf and 4.0 years for loblolly pine, and the range of observed values for each stage transition is several times larger for

TABLE 3.7. Test results for comparisons between tree species of duration of excavation of stage transitions. Stages depicted are substart (SS), start (ST), advanced start (SA) and completed cavity (CP). Comparisons were conducted using the Mann-Whitney U-Test (test statistic U) for the analyses of successfully completed stages, and using Gehan's generalized Wilcoxon Test (test statistic z) for the analyses including censored observations.

Analysis	Cavity population	Stage transition	Test statistic	p	Significance
<i>Analyses of successfully completed stages</i>	FB/MACK	SS to ST	0.0	1.000	N
		ST to SA	24.5	0.013	Y
		SA to CP	419.5	0.426	N
	CNF	SS to ST	28.0	1.000	N
		ST to SA	29.0	0.717	N
		SA to CP	91.0	0.109	N
	CL	SS to ST	102.0	0.284	N
		ST to SA	27.5	0.379	N
		SA to CP	102.0	0.284	N
<i>Analyses including censored observations</i>	FB/MACK	SS to ST	--	--	--
		ST to SA	2.749	0.003	Y
		SA to CP	0.774	0.220	N
	CNF	SS to ST	0.064	0.475	N
		ST to SA	0.066	0.474	N
		SA to CP	0.983	0.163	N
	CL	SS to ST	0.757	0.225	N
		ST to SA	-1.983	0.024	Y
		SA to CP	0.557	0.289	N

longleaf pine (Table 3.5). For CL, the median estimate for the start to the advanced start stage transition is greater (although not significantly so, Table 3.7) for loblolly than for longleaf pine. This translates into estimates for the duration of the entire excavation process that are higher for loblolly (5.5 years) than they are for longleaf pine (4.0 years) (Table 3.5).

Estimates obtained from the analyses that included censored observations were at least three years greater for longleaf pine in two of the cavity populations and less than one year greater for loblolly pine in the third (Table 3.6). Just as they were for the analyses of successfully completed stages, differences were highly significant between species for the duration of the transition between starts and advanced starts on FB/MACK (Table 3.7). The start to advanced start stage was significantly longer for loblolly on CL (Table 3.7), but because the other stages were longer in longleaf, overall excavation time was similar for the two species (Table 3.6).

The distributions reported in Figure 3.1 provide information on the variability inherent to the process of excavation. These distributions include substantial percentages of left-censored data, that is, of observations based on cavities upon which excavation had begun prior to their first being discovered as starts. The values reported should therefore be regarded as (slight) underestimates. The distributions are useful, however, in confirming the similarities and differences between pine species in the duration of the excavation process. The distributions are very similar in shape and in tail length for both CNF and CL, although they are shifted more to the right for loblolly pine. For FB/MACK, however, differences between the pine species are obvious. The distribution for longleaf pine is shifted right, and has a longer tail, compared to that for loblolly pine.

Comparison of Cavity Populations

Median duration of excavation in longleaf pine was essentially identical between the two coastal populations within each analysis, but was consistently higher for FB/MACK (Tables 3.4-3.6). For loblolly pine, excavation time estimates for the Sandhills population were either greater than or comparable to those for the coastal populations (Tables 3.4 and 3.5), except that they were lower in the analyses that included censored observations (Table 3.6). However, duration of excavation of loblolly was underestimated for FB/MACK in this last analysis.

In the analyses of successfully completed cavities, differences between populations approached significance for longleaf pine (Kruskal-Wallis ANOVA, $X^2 = 5.593$, $p = 0.061$), but were not significant for loblolly pine ($X^2 = 2.069$, $p = 0.355$). For the remaining analyses, tests for differences in duration of excavation were again conducted between stage transitions. No significant differences existed between populations for the analyses of successfully completed stages (Table 3.8). For the analyses using censored observations, differences between populations were highly significant only for excavation from the start to advanced start stage in longleaf pine (Table 3.8). Differences in the duration of the entire excavation process in longleaf pine may therefore be significant between populations.

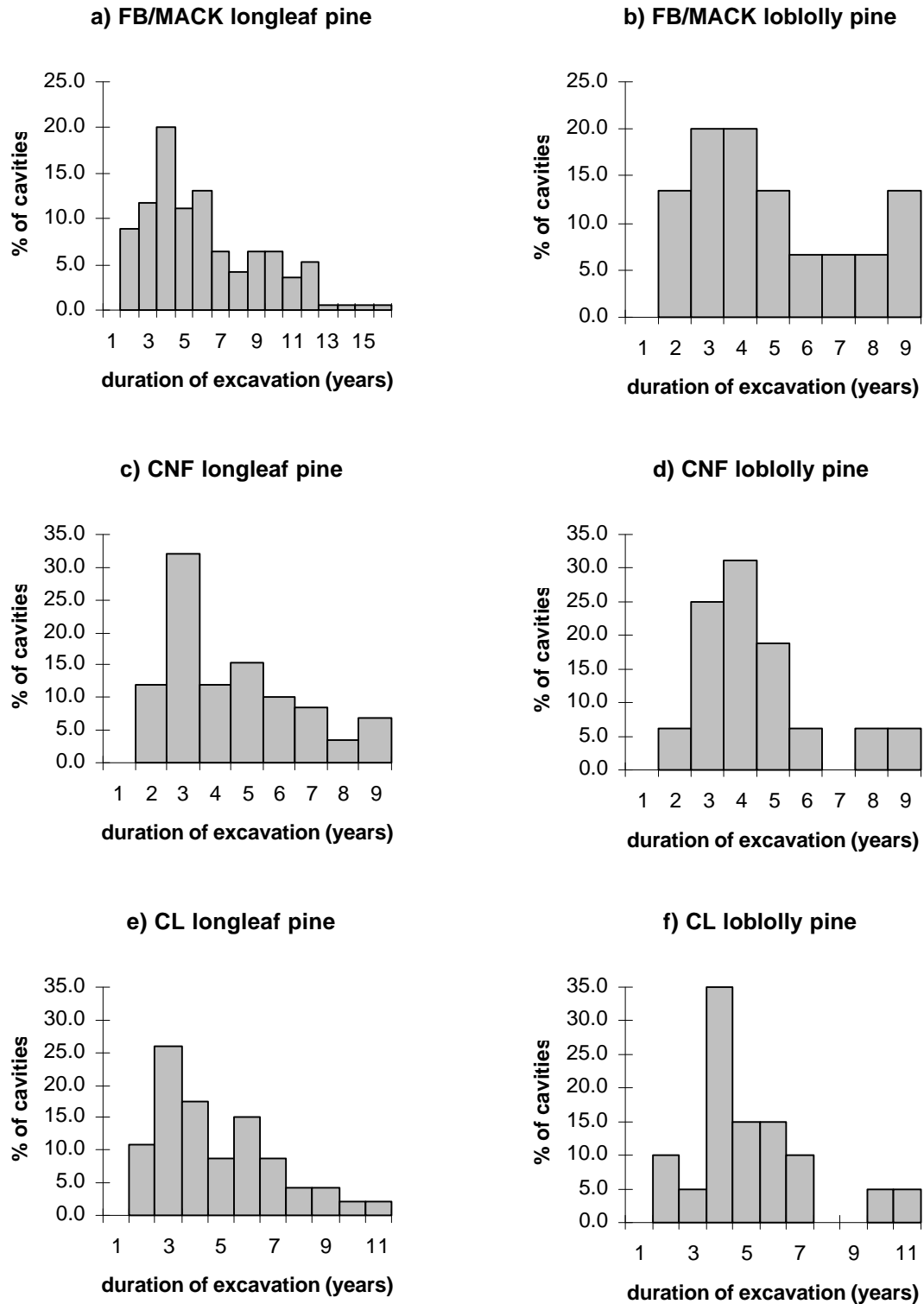


FIGURE 3.1. Percentage distribution of duration of the process of cavity excavation (substart to completed cavity) in a) longleaf pine on FB/MACK (n = 169), b) loblolly pine on FB/MACK (n = 15), c) longleaf pine on CNF (n = 59), d) loblolly pine on CNF (n = 16), e) longleaf pine on CL (n = 46) and f) loblolly pine on CL (n = 20). Includes left-censored data.

TABLE 3.8. Test results for comparisons between cavity populations of duration of excavation of stage transitions. Stages depicted are substart (SS), start (ST), advanced start (SA) and completed cavity (CP). Unless otherwise noted, comparisons were conducted using the Kruskal-Wallis ANOVA (test statistic X^2) for the analyses of successfully completed stages and an extension of Gehan's generalized Wilcoxon Test (test statistic X^2) for the analyses including censored observations.

Analysis	Species	Stage transition	Test statistic	p	Significance
<i>Analyses of successfully completed stages</i>	Longleaf	SS to ST	2.448	0.294	N
		ST to SA	2.338	0.311	N
		SA to CP	2.025	0.363	N
	Loblolly	SS to ST	0.321	0.852	N
		ST to SA	2.860	0.239	N
		SA to CP	2.565	0.277	N
<i>Analyses including censored observations</i>	Longleaf	SS to ST	1.918	0.383	N
		ST to SA	21.984	0.000	Y
		SA to CP	0.165	0.921	N
	Loblolly	SS to ST	0.688*	0.894	N
		ST to SA	3.225	0.199	N
		SA to CP	0.168	0.919	N

*Note: comparison conducted using Gehan's generalized Wilcoxon Test (test statistic z)

Duration of the Different Stages of Excavation

Comparison of Analyses

In the analyses using uncensored observations only, median length of excavation from substart to start was shorter than or equal to the estimates for the other stage transitions (Table 3.5) for both pine species. For longleaf pine, the start to advanced start stage transition was consistently longer than the advanced start to completed cavity transition by a ratio of approximately 2:1. This ratio was more variable for loblolly pine, ranging from 0.5 to 2.0. Differences between stages were not significant for either pine species, however, with the exception of cavities excavated in longleaf pine on FB/MACK (Table 3.9). Each stage differed significantly from all the others in this case (Table 3.10).

In the analyses using censored observations, estimates for the transition between substart and start were consistently the lowest, regardless of the tree species or of the cavity population. However, the ratio of the length of excavation between start and advanced start to that between advanced start to completed cavity was variable between populations and pine species. This ratio ranged from 0.7 to 3.0 for cavities excavated in longleaf and 1.0 to 2.0 for cavities excavated in loblolly pine (Table 3.6). The differences between stages were significant (FB/MACK) or approaching significance (CNF and CL) in longleaf pine (Table 3.9). In all

TABLE 3.9. Test results for comparisons of duration of excavation between stage transitions for analyses of uncensored observations and survival analyses. Unless otherwise noted, comparisons were conducted using the Kruskal-Wallis ANOVA (test statistic X^2) for the analyses of successfully completed stages and an extension of Gehan's generalized Wilcoxon Test (test statistic X^2) for the analyses including censored observations.

Analysis	Cavity population	Pine species	Test statistic	p	Significance	
<i>Analyses of successfully completed stages</i>	FB/MACK	longleaf	28.474	0.000	Y	
		loblolly	1.863	0.394	N	
	CNF	longleaf	3.515	0.173	N	
		loblolly	1.893	0.388	N	
	CL	longleaf	2.579	0.273	N	
		loblolly	3.516	0.172	N	
	<i>Analyses including censored observations</i>	FB/MACK	longleaf	85.017	0.000	Y
			loblolly	- 0.052*	0.479	N
CNF		longleaf	0.575	0.056	N	
		loblolly	3.126	0.209	N	
CL		longleaf	4.904	0.086	N	
		loblolly	7.701	0.021	Y	

*Note: comparison conducted using Gehan's generalized Wilcoxon Test (test statistic z)

TABLE 3.10. Test results for comparisons of duration of excavation in longleaf pine for stage transitions within populations for those significant differences in the analyses of successfully completed stages from Table 3.9. Stages depicted are substart (SS), start (ST), advanced start (SA) and completed cavity (CP). Comparisons were conducted using the Mann-Whitney U Test (test statistic U).

Species	Cavity population	Stage transition	Test statistic	p	Significance
<i>Longleaf</i>	FB/MACK	SS to ST vs. ST to SA	336.5	0.000	Y
		SS to ST vs. SA to CP	1388.5	0.000	Y
		ST to SA vs. SA to CP	1631.5	0.000	Y

populations the substart to start transition differed significantly from the remaining stage transitions (Table 3.11). Differences between the start to advanced start and the advanced start to completed cavity transition were significant only on FB/MACK (Table 3.11). For loblolly pine, differences between stages were significant only for the CL population (Table 3.9). Again, the start to advanced start transition was the longest of the three transitions, but all comparisons of stages at least approached significance (Table 3.11).

TABLE 3.11. Test results for comparisons of duration of excavation for stage transitions within populations for those differences that were significant or approaching significance in the analyses using censored observations from Table 3.9. Stages depicted are substart (SS), start (ST), advanced start (SA) and completed cavity (CP). Comparisons were conducted using Gehan’s generalized Wilcoxon Test (test statistic z).

Species	Cavity population	Stage transition	Test statistic	p	Significance
<i>Longleaf</i>	FB/MACK	SS to ST vs. ST to SA	- 8.824	0.000	Y
		SS to ST vs. SA to CP	- 5.358	0.000	Y
		ST to SA vs. SA to CP	6.035	0.000	Y
	CNF	SS to ST vs. ST to SA	- 2.411	0.008	Y
		SS to ST vs. SA to CP	- 1.715	0.043	Y
		ST to SA vs. SA to CP	1.001	0.158	N
	CL	SS to ST vs. ST to SA	- 1.878	0.030	Y
		SS to ST vs. SA to CP	2.052	0.020	Y
		ST to SA vs. SA to CP	0.519	0.302	N
<i>Loblolly</i>	CL	SS to ST vs. ST to SA	- 2.875	0.002	Y
		SS to ST vs. SA to CP	1.483	0.069	N
		ST to SA vs. SA to CP	-1.859	0.032	Y

Comparison of Tree Species

Differences between pine species in length of excavation appear to lie with the start to advanced start transition. While median values of excavation were roughly equal between species for the analyses of successfully completed stages (Table 3.5), and tended to be greater in longleaf than in loblolly pine when censored observations were included (Table 3.6), the only significant differences were in the length of this particular stage transition. A highly significant difference was found for FB/MACK both when censored observations were included and when they were excluded (Table 3.7). Surprisingly, the length of this stage was significantly greater for loblolly on CL (Table 3.7) for the analyses including censored observations, exceeding that of longleaf by a ratio of 2:1 (Table 3.6).

Comparison of Cavity Populations

When censored observations were excluded, estimates of excavation length between populations were similar for each stage transition, but tended to be slightly higher for FB/MACK (Table 3.5). When censored observations were included, however, estimates for FB/MACK tended to be slightly lower than those for the coastal populations, although values were generally similar (Table 3.6). There were two notable exceptions. For the start to the advanced start transition in longleaf pine, the median value for FB/MACK, at 9.1 years, was more than twice that for the coastal populations (Table 3.6). This difference was highly significant (Table 3.8). For the same stage transition in loblolly pine, the median value on CL, at 6.0 years, was two to three

times as high as those for the other populations. This difference was not significant, however (Table 3.8).

Discussion

Patterns of Cavity Excavation

In the only other study to quantify cavity excavation by the red-cockaded woodpecker, Conner and Rudolph (1995a) estimated that excavation of cavities in eastern Texas requires approximately six years to complete in longleaf and two years in loblolly pine. The results

presented here indicate that the long excavation times reported by Conner and Rudolph are not aberrant: depending on the cavity population, cavities in longleaf pine were estimated as requiring a median of nine to thirteen years, and cavities in loblolly pine roughly four to ten years, to excavate. Median estimates in my study are thus up to twice as long as the mean estimates reported for longleaf pine by Conner and Rudolph, and up to five times as long as those for loblolly pine.

Given the enormous time investment required to excavate cavities in living trees, it is surprising that, of all the excavation attempts made by the woodpeckers, relatively few were carried through to completion. Only 20-30 % of all excavation attempts result in completed cavities, and more starts were abandoned than completed in two of the three cavity populations (Table 3.3). The process of cavity excavation in this woodpecker species has in fact proven to be far from straightforward: non-completed cavities may be excavated irregularly over the course of several years before being finally completed, and duration of excavation, both of the entire process and of its component stages, appears to be highly variable both between and within cavity populations. These and other issues are discussed in the sections that follow.

Cavity Excavation and the Cooperative Breeding System

The results of my study support the hypothesis that cavities in living pine trees require years to complete and lend indirect yet powerful support to the ecological constraints model for the evolution of cooperative breeding in the red-cockaded woodpecker. There is little doubt that cavities represent a critical resource to red-cockaded woodpeckers. Cavities are necessary for a woodpecker's survival, providing shelter from temperature extremes (McFarlane 1992) and from natural predators such as climbing rat snakes (*Elaphe* spp.; Jackson 1974, Rudolph et al. 1990a). As nest sites, cavities also play a critical role in reproduction. The presence of viable cavities on a territory acts as a primary determinant of territory quality, as evidenced by the results of creation of territories following Walters et al.'s (1992b, Copeyon et al. 1991) experimental provisioning of unoccupied habitat with artificial cavities. The length of the excavation process is thus implicated in a system in which reproductively mature males compete for breeding vacancies on existing territories rather than creating new territories through the excavation of cavities on unoccupied habitat. Given that the length of the excavation process may exceed a woodpecker's lifetime, it is

not surprising that colonizing a new territory without cavities is not normally a viable option for this species.

Competition for breeding vacancies occurs in two ways: (1) individuals defer natal dispersal and compete for openings on their natal territory or in neighboring territories, dubbed ‘stay and foray’ (Brown 1987), and (2) individuals disperse in their first year and seek out vacancies elsewhere, or ‘disperse and search’ (Brown 1987). Individuals that stay and foray thus become helpers and roost in cavities on their natal territory, while individuals that disperse and search either occupy a breeding vacancy or become floaters (Walters et al. 1988). Floaters do not affiliate with a particular group (Walters 1990), and thus do not enjoy residency on any territory. Instead, they continue to float until they eventually occupy a breeding vacancy or suffer mortality (Walters et al. 1988).

Not much is known about the floater lifestyle in this species, but birds are known to survive several years of floating to go on to become breeders (Walters, unpublished data). This begs the question of how a bird without ownership of a cavity necessary for its survival manages to survive. It has been documented that some floaters have become helpers to breeding birds to which they are unrelated (Walters 1990), thus securing access to cavities on the territory on which they establish residence. Others are known to affiliate with particular groups of woodpeckers and roost in their cluster (Hooper 1983, Jackson 1994) despite repeated aggression toward them (Walters 1990). Others may exhibit a more nomadic lifestyle, ‘sneaking’ into cavities, fighting for access to cavities, or roosting in the open when not occupying vacant cavities. Red-cockaded woodpeckers are capable of roosting in the open for prolonged periods (Hooper 1983, Walters et al. 1992b), hence floaters may adopt this strategy when access to cavities is restricted. However, it appears that floaters are often capable of obtaining access to cavities, so that a floater’s probability of survival is ultimately greater than it would be for a bird setting out to colonize a new territory. The question may thus not be one of survival, but one of reproduction. A comparison between average duration of cavity excavation to completion and average length of time to first breeding of both dispersing and non-dispersing birds would further clarify the issue of why suitable habitat lacking cavities is avoided by dispersing fledglings.

Ecological constraints relating to the absence of cavities from habitat clearly discourage individuals from colonizing new territories. This only offers a partial explanation as to why delayed dispersal arose for this species, however, given that the floater strategy appears to be a viable one. Just as deferring dispersal and competing for breeding vacancies on one’s natal territory or on neighboring territories can lead to eventual breeder status, so can dispersing and floating. Delayed natal dispersal is in fact rarely exhibited by females (Walters et al. 1988). Using demographic data collected from the Sandhills woodpecker population, Walters et al. (1992a) evaluated a model of the evolution of delayed dispersal and reproduction based on selection between the ‘stay and foray’ and ‘disperse and search’ tactics. The results indicated that the fitness of individuals exhibiting the former behavior equaled or exceeded that of individuals opting for the latter. The fitness pay-offs of both tactics relative to one another indicate that each tactic is under similar selection pressures, and thus explain why both tactics persist. The coexistence of the two contrasting choices has prompted the labeling of the woodpecker as a ‘primitive’ cooperative breeder (Walters 1990), as a complete switch toward cooperative breeding,

characterized by the dispersal of few or no birds, has not been made. In effect, the cooperative aspect of the breeding system hangs in the balance between the two strategies.

The Stages of Excavation

Four stages of excavation and three transitions between them were identified in this study. The first transition, that between the substart and the start stage, was consistently the shortest for both pine species, but the length of the two remaining transitions varied between populations. Statistical differences between these transitions existed only in one cavity population (FB/MACK) for longleaf pine and in another (CL) for loblolly: length of excavation from the start to the advanced start stage was three times longer for longleaf and twice as long for loblolly than it was from the advanced start to the completed cavity stage. These results indicate that excavation of both stage transitions is subject to great variability, but that when differences in duration between them do exist, it is the transition from start to advanced start that is the longer of the two.

Excavation to both the start and to the advanced start stage takes place almost exclusively in the sapwood layer of the pine. Wounding of the sapwood results in the flow of resin, or sap, which acts as a defense by trapping infesting insects and forming a protective layer against water loss and fungal infection (Conner and Rudolph 1995a, Stern 1988). As the woodpeckers cannot effectively excavate through flowing sap, and as contact with sap may result in mortality when woodpeckers become stuck (Copeyon 1990), excavation is often suspended (Conner and Rudolph 1995a). Excavation can resume without stimulating additional sap flow once the sap hardens: this occurs after the sapwood has become saturated through the process of resinosis (Conner and Rudolph 1995a). This process may require one or more months (Conner and Rudolph 1995a), but its timing has not been methodically quantified. The greater period of time required to excavate a cavity to the start stage is consistent with the fact that the depth of a start is greater than that of a substart.

Excavation from the advanced start stage to completion, in contrast, is confined to the heartwood, which is composed of dead tissue with low moisture content (Shigo 1986), and is thus harder to excavate than sapwood (Conner and Rudolph 1995a). Because excavation through the heartwood does not result in sap production, however, no constraints relating to time are imposed on excavating woodpeckers. Constraints instead are associated with difficulty of excavation, which is greatly affected by whether or not the heartwood is infected by red heart fungus. Infected heartwood is significantly easier to excavate than is sound heartwood, so that excavation of infected heartwood is expected to require less time. It is well documented that the woodpeckers select trees with red heart infection for excavation (Jackson 1977b, Conner and Locke 1982, Hooper 1988, Hooper et al. 1991, Rudolph et al. 1995), although the cues used by the woodpeckers to detect infection are undetermined. Abandonment of excavation in some cases may be related to the absence of heart rot, although heart rot is not a prerequisite for successful excavation (Beckett 1971, Conner and Locke 1982, Hooper 1988, Hooper et al. 1991).

The mechanics of the excavation process in conjunction with the physical characteristics of the tree clearly impose limitations on excavation rates. Given the nature of these constraints, it is expected that excavation from start to advanced start will be the lengthier transition, as it is

characterized by flowing sap that physically impedes the woodpeckers from excavating. This is consistent with the results for which differences were detected, but inconsistent with those for which they were not. That some results were not different can be explained by the high degree of variability in excavation rates of the two stage transitions (especially that of the start to advanced start transition). This issue is explored further in the next section.

Differences in Duration of Excavation

The distribution of excavation times reported in this study is characterized not only by a large mean, but also by large variance. Although some cavities in longleaf were excavated in 15 years (Table 3.6), other required only two years to complete, from start to finish (Table 3.3). As discussed above, most of this variability occurs at the start and advanced start stages, excavation of which is subject to constraints relating to the physical characteristics of cavity trees. These constraints are themselves prone to variation, some of which likely occurs at the level of the individual tree. Strength of sap flow, thickness of sapwood, and presence of red heart fungus may all vary among individual trees. It is possible, for example, that duration of excavation past the advanced start stage is shorter than that to the advanced start stage only in those cavities afflicted with heart rot. Variation probably exists at other levels as well, as strength of sap flow is documented to differ between tree species (Hodges et al. 1977 and 1979, Hicks 1980) and all three variables may vary among populations (see below).

It is unlikely that variation in the physical characteristics of individual trees can entirely explain variability in excavation rates within the same stage in the same tree species, however. An additional major factor contributing to this variability is likely the effort expended by the woodpeckers. Reactivation rates indicate that non-completed cavities in longleaf pine have sat idle for as long as twelve years, and cavities in loblolly six years, before excavation on them resumed. This is surprising, as delaying excavation exposes these cavities to a greater probability of usurpation by competing species (McFarlane 1992) or to loss prior to completion. This may not be a problem for red-cockaded woodpeckers, however, as relatively low proportions of their non-completed cavities are lost (Table 3.3). It is also common for several non-completed cavities at different stages of excavation to exist simultaneously in a cluster (pers. obs., Walters, pers. comm.). All of this suggests that the woodpeckers exert varying degrees of effort in different years, and that their effort is distributed over many cavities at one time. Variation in effort may be controlled by several variables, including variation among individual birds, in the number of birds available to excavate in a group, and in the need for new cavities. The latter possibility was proposed by Conner and Rudolph (1995a), who reported that advanced starts were sometimes excavated to completion following one or more years of inactivity. Based on this observation, they suggested that excavation may be suspended until the need for a new nest cavity arises during the breeding season following loss of the breeding male's roost cavity, which normally also serves as the nest (Jackson 1994). Their contention is not supported by my study, as a large proportion of nest cavities were not used as nests in the first breeding season following completion (see Chapter 4). However, excavation could still be occurring as a response to the need for cavities for roosting, rather than nesting.

If woodpeckers are completing cavities in response to need, it is expected that excavation would be suspended once cavities had been excavated to a point where they could be quickly completed once the need arose. In order that future excavation would not be constrained by sap flow, this point would be the advanced start stage. Unfortunately this prediction can not be tested here, although it is expected that the reactivation rates for advanced starts would be higher than those for other stages if the woodpeckers 'intend' on eventually completing excavation on these cavities. Reactivation probabilities for advanced starts are generally higher (Tables 3.1-3.2), although starts are sometimes reactivated following longer periods of inactivity. The factors that are ultimately responsible for variation in excavation effort are explored in greater detail in Part II (Chapter 6).

Differences Between Tree Species

Conner and Rudolph (1995a) found excavation in longleaf pine to require 3.5 times longer than it does in loblolly. The results presented here are more equivocal. Overall, the trend is that estimates for longleaf are longer (by up to 2.5 times) or at least equal to those for loblolly pine (Table 3.6). However, given the range of estimates, it is difficult to generalize about differences between the two species. The species are known to differ in sap-production potential, with longleaf pine being the greater producer (Hodges et al. 1977 and 1979, Hicks 1980). It is perhaps telling, then, that differences in duration of excavation are associated almost exclusively with the transition between the start and the advanced start stage. Surprisingly, the length of excavation of this stage transition was not always greater in longleaf pine, as excavation on the CL study site took twice as long in loblolly pine. Explanations based on sap flow thus can not be generalized to all three cavity populations, although it is possible that other factors are confounding what would otherwise be visible trends on some of the study areas. Sap production takes place in the pine needles (Wahlenberg 1946, Schopmeyer and Larson 1955), as well as in other parts of the tree (Stern 1988), which suggests that the size of the pine's crown can influence rates of sap flow. Variation in the mean crown size of cavity trees of the two pine species relative to one another may exist among the cavity populations, as climatic (King 1972, Kalkstein 1976) and edaphic factors that influence growth (Belanger et al. 1977, cited in Rudolph and Conner 1995, Hicks et al. 1978, cited in Rudolph and Conner 1995) may vary between and within geographic locations. Sap flow may thus affect duration of excavation to a greater extent in either species depending on the cavity population.

Correlations between crown-bole ratio and rate of sap flow have yielded conflicting results in other cavity populations, however: Bowman and Huh (1995) found peak resin flow to be associated with median crown-bole ratios, while Hodges et al. (1979) found resin flow and crown-bole ratio to be only weakly related. Although they did not look at this relationship directly, Conner and O'Halloran (1987) found significantly higher crown-bole ratios in cavity trees than in unused trees. However, Locke et al. (1983) found the opposite relationship in woodpecker territories compared to unused habitat. Differences between species in rate of sap flow, especially as they relate to the factors that influence sap production and variation in these factors among geographical locations, thus do not represent the best explanation of differences between pine species in duration of excavation.

Conner and Rudolph (1995a) speculated that differences in the incidence of fungal decay among pine species may have led to differences in excavation rates between them. This explanation is unlikely in my study, as differences did not exist in excavation rates at the advanced start to completed cavity transition, where excavation takes place exclusively in the heartwood. What accounts for the differences between species reported here remains unresolved at this point.

Differences Between Cavity Populations

It is clear from the differences between cavity populations in my study, as well as the differences between my study and the populations studied by Conner and Rudolph (1995a), that duration of excavation can vary among cavity populations. Although a great deal of variability in excavation rates exists within each population, variability between populations appears to be due in great part to variation at the start to advanced start transition. In longleaf pine cavities in the Sandhills, excavation of this stage transition alone requires as much time as does the entire excavation process in the coastal populations (Table 3.6). Similarly, excavation of this stage transition in loblolly pine on CL requires as long or longer as excavation of the average cavity from start to finish does in the other cavity populations. Given the importance of the role that this stage transition plays in accounting for differences both between cavity populations and tree species, future research on excavation dynamics, while encompassing the entire excavation process, should focus especially on this particular stage transition.

As explanations relating to fungal infestation have proven inadequate and explanations relating to sap flow are highly speculative, variability in effort on the part of the woodpeckers is again invoked as a likely explanation. Whether effort is a response to the need for cavities is again questionable. If the need for cavities were influencing excavation effort, it would be expected that duration of excavation be shorter in those populations with greater cavity losses, as the woodpeckers would be responding to need by excavating cavities faster. Excavation in longleaf is in fact shortest in the coastal populations, where the loss of longleaf cavities is proportionally higher than on FB/MACK (see Chapter 5). However, losses of loblolly cavities from the cavity population with the longest excavation times (CL) are proportional to losses from the other cavity populations, indicating that a response to need may not be operating. The trends are nonetheless suggestive, as the majority of cavities in all three populations are excavated in longleaf pine (see Chapter 5). Other variables that may differ between the study areas, such as the size of the woodpecker population relative to the number of available clusters and reproductive output leading to recruitment of helpers, may also help explain differences in excavation times.

Duration of Excavation and Survival Analysis

Exclusion of censored observations from longitudinal studies such as this one clearly lead to biased results. It was evident in comparing the analyses based exclusively on successfully completed stages to the analyses that included censored observations that the former produced underestimated results. Estimates from the survival analyses were, in some cases, more than twice as high as those from the other analyses.

Although inclusion of censored observations leads to results that are more reliable than are estimates based on the exclusion of such data, survival analysis is not without its shortcomings in estimating rates of excavation. The factor with the greatest potential to affect the results is the choice of which observations to include in the analyses. Non-completed cavities determined as having a low likelihood of being excavated to the next stage were excluded in order to avoid inflation of the mean and of the median. However, other factors that could influence excavation, such as the sap-production potential of a tree and the degree of encroachment of a cavity tree by the surrounding midstory, were not considered. Because the presence of fresh resin around a cavity decreases the vulnerability of a cavity to arboreal predators (Jackson 1974, Rudolph et al. 1990a), abandonment of excavation could result if a tree fails to produce sufficient quantities of sap before excavation is even completed. Excavation may also be permanently suspended as a result of a cavity becoming accessible to predators via the surrounding vegetation (Locke et al. 1983, Hovis and Labisky 1985, Conner and Rudolph 1991, Loeb et al. 1992). Similarly, the calculation of reactivation rates may have led to the inclusion in the analyses of certain cavities with low probabilities of being excavated further. No attempt was made to differentiate between non-completed cavities that were inactive for similar periods of time but upon which excavation had been proceeding for different periods of time. Although the probability of reactivation likely differs between such cavities, this level of distinction was not made because it would have resulted in sample sizes too small for the calculation of reliable reactivation rates. In addition, the observed level of activity of non-completed cavities used to calculate reactivation rates is based on updates taken once yearly during the breeding season, but excavational activity peaks in the later part of the breeding season and in the months following (Walters, pers. comm.). The duration of inactivity experienced by a cavity is thus subject to potential overestimation. This would have affected the calculation of the rates of reactivation and could have resulted once more in the inclusion in the analyses of cavities upon which excavation had been abandoned.

Chapter 4: Dynamics of Cavity Use

Methods

Patterns of Cavity Use

Use of cavities by red-cockaded woodpeckers can be irregular over periods of years, both for roosting (Conner and Rudolph 1995a) and for nesting. Variation in use may also exist within years in the former case, as adults residing on a territory may switch cavities over the course of time, and fledglings may roost in previously inactive cavities in the months preceding dispersal from their natal territory (Walters, pers. comm.). Cavity occupancy, which is here synonymous with cavity use, is generally inferred by the presence of certain physical characteristics of a cavity (see Chapter 2), rather than by direct observation of the presence of a roosting individual in a cavity. Active cavities are reasonably assumed to be occupied regularly by a roosting woodpecker at night. Typically only one adult roosts per cavity (Jackson 1994). The absence of these physical characteristics signifies that a cavity is inactive, and thus not being used for roosting. Use of a cavity for nesting is inferred directly by the presence in the cavity of nesting material, eggs, nestlings, and incubating adults.

As mentioned previously, the data upon which the analyses are based were collected each year during the breeding season. Given the dynamics of cavity use within groups of woodpeckers, a cavity that appears to be occupied during the breeding season may be vacant a few months later. Similarly, a cavity that is inactive during the breeding season may be activated and used for roosting for a few months during winter (Walters, pers. comm.). Thus duration of use of cavities for roosting, while measured in years, is in fact not necessarily representative of year-round use, but rather of use during the breeding season. Cavity occupancy may change within a breeding season, however (Walters, pers. comm.), and cavities are generally updated only once during this period. The measures of use dealt with in this chapter are thus more indicative of broad temporal patterns rather than of the dynamics of use that occur on a finer temporal scale.

Unlike roosting, nesting is a seasonal activity confined to the woodpecker's breeding season (Walters 1990). Because only the breeding pair is typically engaged in reproductive activities (Haig et al. 1994), there is only one nest cavity per cluster during this period (barring re-nesting following nest failure). Cavities are therefore unequivocally identified during the breeding season as either being used or not used as nest cavities. Estimation of duration of nest use thus is not affected by the same factors that confuse the estimation of duration of use of cavities as roost cavities.

Mean and median duration of use of completed cavities by the red-cockaded woodpecker were calculated in years for each of the cavity populations. Separate analyses were conducted for the use of cavities as roost cavities and as nest cavities.

Analysis of the Duration of Cavity Use For Roosting and Nesting

Description of Analyses

Because of the irregularity in use of cavities by red-cockaded woodpeckers between years, three related measures of use were estimated using survival analysis in order to obtain a more comprehensive picture of use patterns. The measures are defined as follows: (1) the span of years a cavity is used is measured as the period from and including the first year a cavity is used to the last year it is used; (2) the total number of years of use is measured as the sum of the years of use within the span of years during which a cavity is used; and (3) the number of consecutive years of use is defined as the period from and including the first year a cavity is used to the first year it is not used. For roosting, cavity use is defined according to whether the cavity is active or inactive. For nesting, it is defined by the presence or absence of a nest in the cavity.

Two sets of analyses were conducted for use of cavities for roosting and two for use of cavities for nesting based on the measures described above. The first served to estimate duration of cavity use under the full range of conditions encountered by red-cockaded woodpeckers in the study areas. Such conditions include factors external to the cavity that render the cavity unsuitable, namely enlargement of cavities by other woodpecker species, tree death, cavity breakage and territory abandonment (see Chapter 5). The second set excluded cavities lost to these factors in order to estimate duration of use under a set of 'ideal' conditions under which the cavity remains available. Comparison of the results of these two sets of analyses may indicate the role that external factors that render cavities unsuitable play in the dynamics of cavity use.

The use of artificially drilled cavities and cavity inserts has become a popular management tool to supplement territories that have insufficient numbers of suitable, naturally excavated cavities. Duration of use was calculated for artificial cavities for the first set of analyses and compared to that of naturally excavated cavities in order to evaluate the potential for use of the former by the woodpeckers. The measures of use of naturally excavated cavities were also compared among cavity populations and pine species. As discussed in Chapter 3, cavity excavation normally occurs during the post-breeding period of the year. Duration of use for roosting for each cavity was thus measured from the first breeding season following the year of cavity completion onward.

As stated earlier, the measures of duration of use of cavities for roosting are based on a cavity's being either active or inactive. However, cavities are sometimes assigned 'possibly active' status when checked (see Chapter 2) in order to designate a period that is transitional between use and non-use. Possibly active cavities generally are used only occasionally as roosts during the breeding season when one or more of the active cavities are temporarily unavailable (Walters, pers. comm.). Because the calculation of duration of use outlined above does not account for possibly active status, these cavities were assigned inactive status. Thus the calculations relate to regular use of a cavity during a breeding season and may underestimate the duration of intermittent use at the end of a cavity's lifespan. Underestimation is also possible in cases in which cavity trees died. Cavities were generally not updated following a tree's death. The period of use of cavities in trees that died was thus subject to potential underestimation,

especially as trees were assumed to have died during the breeding season of the year in which the death was recorded (see Appendix).

Cavities that are active are not always in use by red-cockaded woodpeckers. A host of other species, mostly avian but including southern flying squirrels (*Glaucomys volans*), may usurp a cavity (Dennis 1971, Jackson 1978, Carter et al. 1989, Rudolph et al. 1990b). Occupancy generally tends to be temporary, although honey bees (*Apis mellifera*) can occupy a cavity for several years. Occupancy by other species was not controlled for in these analyses, but any effects it might have on the estimation of each of the three measures of use is slight.

Criteria for Inclusion of Data into Analyses

In order to avoid using left-censored data, both sets of analyses were limited to those cavities that (1) were observed passing through a non-completed phase and (2) for which the year of completion of excavation was known. During field updating, cavities were sometimes judged to have been ‘recently completed’, although they may not have been previously recorded as non-completed cavities. These cavities were excluded because their year of completion was based on the judgment of the observer rather than on knowledge of the cavity’s progression through the different stages of excavation in previous years. Also excluded were cavities that were not updated consistently during each breeding season from the year of completion to (1) the last year of a study, or (2) the year in which they were lost or are denoted as relicts (see next section). Cavities that were never active following completion were also not included. In addition, cavities whose status as nests was undetermined at any point were excluded. This occurred when completed cavities belonged to clusters that were not checked for nests every year, or when a nest tree with multiple cavities was identified but no data on the identity of the nest cavity were recorded. Cavities in clusters that were not checked consistently were included in the analyses as lost-to-follow-up, however, if the clusters in question were not checked in consecutive years that included the last year of a study.

Common cavities were omitted from the analyses of use of cavities for roosting, as their activity status in any given year was confounded by differences in the activity status of each entrance. Common cavities were included in the analyses of use of cavities for nesting, however, as the presence or absence of a nest in a common cavity is unequivocal. Cavities fitted with restrictors were excluded from all analyses because direct management activities have the potential to affect the duration of cavity use. Cavities in abandoned clusters were included as inactive cavities for the years in which the cluster was abandoned in the first set of analyses for roosting. Although these cavities were sometimes found to be active during updates, they were likely occupied by woodpeckers that had not established residency in the cluster.

Analyses of artificial cavities likewise included only those cavities meeting the criteria established above. Because wire mesh screens are installed over cavity entrances in order to prevent access during periods of sap flow, duration of use was measured from the first breeding season following removal of a screen onward. Cavities were excluded from the analyses if a screen was removed during the breeding season and the cavity was not subsequently updated

during that same breeding season. Small sample sizes precluded the analyses of duration of use of artificial cavities under ideal conditions.

In the analyses of use of cavities for roosting, cavities were considered unsuitable for woodpeckers in the year of their loss, regardless of whether that loss was recorded during or following the breeding season, because it was unknown exactly at what point the loss occurred. Cavities that were excavated to completion in the year of their loss were thus excluded from the analyses. However, whether or not cavities were used for nesting in the year of their loss was known, so that no cavities were excluded from the analyses of use of cavities for nesting on this basis.

Survival Analysis

Censored data were included in the calculation of all three measures of duration of use. Observations used in the calculation of duration of continuous use were assigned uncensored status if a cavity became inactive (for roosting) or underwent a period of non-use as a nest (for nesting), or if it was lost (for the set of analyses that included all cavities, regardless of fate). The latter criterion was also used to assign uncensored status to cavities for the other measures of use, as loss of a cavity typically resulted in permanent abandonment. As discussed previously, cavity loss occurred when a cavity tree died, when the section of tree in which the cavity was excavated was physically separated from the rest of the tree, and when a cavity healed over (see Chapter 5 for a more detailed explanation of cavity loss).

Relict cavities were likewise assigned uncensored status in the analyses, as their probability of being used again is very low (Walters, pers. comm.). While reactivation of relict cavities does occur, it is a rare event in these cavity populations. Observations of cavity use based on relict cavities that were reactivated were considered censored. Enlargement of cavities by other woodpecker species can result in cavity abandonment by red-cockaded woodpeckers (Carter et al. 1989). Because patterns of use of enlarged cavities were not examined, cavity enlargement was not used as a censoring variable in the analyses that included all cavities.

The potential for intermittent use of cavities complicated the estimation of duration of use for both the span of years used and the total number of years used. For the analyses of use of cavities for roosting, those cavities that were inactive for one or more consecutive years up to and including the last year of a study were problematic, as it is not known whether they will be used again in the following years. In order that censoring status could be assigned to such records, a series of reuse rates was computed for each set of analyses. The reuse rates represent the proportion of completed cavities that are used again by red-cockaded woodpeckers following a period of inactivity. The rates were calculated based on a sample of eligible cavities undergoing a period of inactivity. Cavities were eligible if the breeding season in which they first became inactive was known and if they were updated consistently during the breeding season of each year for the entire length of the inactive period. The assumption was made that cavities on FB and MACK for which data were not recorded in some years were updated during those years and found to be inactive. This assumption is reasonable because the field protocol for those collecting

these data was to take data on all active cavities, and then take data on additional inactive cavities as time permitted. The percentage of cavities for which the assumption was used was 23.7 %.

For the analyses of use of cavities for nesting, reuse rates represent the proportion of nest cavities that are used again as nests following periods of non-use of various lengths. Calculation of these rates was based on all cavities that underwent periods of non-use as nest cavities, regardless of whether the year of completion of the cavity is known. Included were only those cavities for which (1) the year marking the beginning of a period of non-use was known, and (2) nesting status was recorded every year for the entire length of the period of non-use, unless the cavity qualified as lost-to-follow-up.

Only the first period of inactivity and of non-use as a nest meeting the above criteria was included in the calculations of reuse rates for those cavities that underwent multiple independent bouts of inactivity or of non-use, respectively. Observations based on common cavities were included for the calculation of reuse rates both for nesting and roosting. In the latter case, they were included only if the period of inactivity meeting the criteria occurred prior to the cavities becoming common. Relict cavities were included as inactive cavities. Cavities that were restricted were excluded.

Reuse rates were calculated separately for each pine species and for each cavity population (except for FB and MACK, which were combined due to small sample sizes on MACK). Given the small sample sizes involved, separate reuse rates could not be calculated for artificial cavities. Based on the rates, the appropriate proportion of cavities that would not be used again for each period of inactivity and for each period of non-use as nests was randomly designated as uncensored observations, and the remainder as censored observations.

Results

Because of the distribution of censored observations in the samples analyzed, medians could not be calculated for the majority of the measures of use of cavities for roosting. Means are instead used as estimators of use for these analyses, and the 25th percentile, marked with a double asterisk, is reported in place of medians. For the analyses of duration of cavity use as nest cavities, both mean and medians were successfully estimated. Mean and median estimates are similar to one another, but means are used as estimators in order to be consistent with the analyses of use of cavities for roosting.

Analysis of the Duration of Use of Cavities as Roost Cavities

Naturally Excavated Cavities

Red-cockaded woodpeckers use their cavities as both roosts and nests for lengthy periods spanning several years. Reuse rates for roosting for each of the cavity populations are reported in Tables 4.1 and 4.2. When all cavities were included, cavities in longleaf pine were estimated to

be used for a mean of 4.6 to 8.3 years (depending on the population), 4.0 to 8.2 of which were continuous, over a span of 4.6 to 9.0 years (Table 4.3). Cavities in loblolly pine, in contrast, were used for a mean of 1.8 to 3.6 years, 1.7 to 4.9 of which are continuous, over a span of 1.8 to 3.6 years (Table 4.3). Estimates of duration of continuous use of loblolly cavities were larger than those of the remaining measures due to the distribution of censored observations in the data. This, together with the fact that the median could not be calculated in the majority of cases, strongly suggests that true duration of use is substantially longer than the estimates indicate. In most cases, estimates of the 25th percentile are in effect similar to the mean estimates, which are in turn restricted in every case but one. Cavities were in fact still being used in longleaf pine after fourteen years and in loblolly pine after ten (Table 4.3).

As is evident from the range of values reported above, duration of use of cavities appears to differ between the two pine species. Cavities excavated in longleaf were used approximately two to three times as long as cavities in loblolly pine for each of the measures of use (Table 4.3). Differences between species were significant for all measures except for that of duration of

TABLE 4.1. Reuse rates of roost cavities in longleaf and loblolly pine following periods of non-use of various lengths. Includes all cavities suitable for analysis regardless of cavity fate.

Species	<i>FB/MACK</i>			<i>CNF</i>		<i>CL</i>	
	No. years inactive	Sample size	Reuse rate	Sample size	Reuse rate	Sample size	Reuse rate
<i>Longleaf Pine</i>	1	412	0.415	115	0.261	91	0.374
	2	195	0.292	66	0.136	46	0.196
	3	126	0.230	45	0.133	31	0.161
	4	87	0.322	28	0.000	22	0.000
	5	57	0.211	18	0.111	17	0.059
	6	43	0.070	11	0.091	14	0.071
	7	34	0.029	8	0.000	10	0.000
	8	25	0.080	0	--	7	0.000
	9	23	0.000	0	--	2	0.000
	10	17	0.000	0	--	1	0.000
	11	17	0.059	0	--	0	--
	12	15	0.067	0	--	0	--
	13	12	0.000	0	--	0	--
	14	7	0.000	0	--	0	--
<i>Loblolly Pine</i>	1	31	0.387	44	0.159	29	0.276
	2	13	0.333	26	0.115	16	0.125
	3	5	0.200	17	0.176	10	0.000
	4	4	0.500	10	0.100	9	0.000
	5	1	0.000	8	0.125	5	0.000
	6	0	--	4	0.000	4	0.250
	7	0	--	1	0.000	3	0.000
	8	0	--	0	--	2	0.000
	9	0	--	0	--	1	0.000

TABLE 4.2. Reuse rates of roost cavities in longleaf and loblolly pine (combined) following periods of non-use of various lengths. Does not include cavities on trees that died, cavities that broke, cavities that were enlarged or cavities on territories that were abandoned after the cavity was complete.

No. years inactive	<i>FB/MACK</i>		<i>CNF</i>		<i>CL</i>	
	Sample size	Reuse rate	Sample size	Reuse rate	Sample size	Reuse rate
1	296	0.517	48	0.396	42	0.595
2	119	0.403	21	0.286	12	0.583
3	63	0.317	9	0.222	4	0.250
4	37	0.459	4	0.000	3	0.000
5	20	0.250	3	0.000	3	0.000
6	14	0.214	1	0.500	2	100.0
7	10	0.100	1	0.000	0	--
8	8	0.125	0	--	0	--
9	7	0.000	0	--	0	--
10	5	0.000	0	--	0	--
11	5	0.200	0	--	0	--
12	3	0.333	0	--	0	--
13	3	0.000	0	--	0	--

continuous use in one of the cavity populations, CL (Table 4.4), for which the mean estimate for loblolly pine slightly exceeded that for longleaf pine (Table 4.3). Differences between pine species were greatest on CNF, where the ratio of duration of use was close to 3.0, somewhat lower on FB/MACK, where the ratio was closer to 2.0, and smallest on CL, where the ratio was under 2.0.

The estimated means for each pine species differed between populations. Values for the coastal populations were closer to one another than they were to values for FB/MACK. For longleaf pine, duration of cavity use for each of the measures was approximately twice as long for the Sandhills than it was for either of the coastal populations (Table 4.3). For loblolly pine, values for CL were intermediate between those of the other two cavity populations, while values for the Sandhills were twice as great as those for CNF for both total use and span of use, and more than twice as great for continuous use. Interestingly, differences between populations were significant only for longleaf pine (Table 4.5). The woodpeckers thus appear to utilize cavities in longleaf pine for longer periods of time in the Sandhills than on the coast, but not cavities in loblolly pine.

Elimination from the analyses of those cavities that do not remain suitable in order to examine duration of use under ideal conditions left no uncensored observations for the majority of these analyses. Therefore only duration of continuous use of longleaf pine could be estimated (Table 4.6). Elimination of cavities that become unsuitable had a significant effect on duration of continuous use for FB/MACK (Gehan's generalized Wilcoxon test, $z = -2.637$, $p = 0.004$) and CL ($z = -2.033$, $p = 0.021$) and a nearly significant effect for CNF ($z = -1.516$, $p = 0.065$). These differences are not obvious when comparing means and medians (Tables 4.3 and 4.6), but do

TABLE 4.3. Three representative measures of duration in years of use of cavities for roosting. Includes all cavities suitable for analysis regardless of cavity fate.

Cavity population	Measure of use	Species	n	% censored obs.	Mean	Median	Min.	Max.
<i>FB/MACK</i>	Span of years used	Longleaf	163	80.4	9.0*	11.7	1.0	14.0
		Loblolly	15	66.7	3.6*	3.3**	1.0	10.0
	Total years used	Longleaf	163	80.4	8.3*	7.8**	1.0	14.0
		Loblolly	15	66.7	3.6*	3.3**	1.0	10.0
	Years of continuous use	Longleaf	163	60.7	8.2*	8.0	1.0	14.0
		Loblolly	15	26.7	4.7	4.0	1.0	10.0
<i>CNF</i>	Span of years used	Longleaf	83	81.9	5.1*	3.8**	1.0	7.0
		Loblolly	32	71.9	1.8*	1.0**	1.0	7.0
	Total years used	Longleaf	83	81.9	5.1*	3.7**	1.0	7.0
		Loblolly	32	71.9	1.8*	1.0**	1.0	7.0
	Years of continuous use	Longleaf	83	69.9	4.5*	2.5**	1.0	7.0
		Loblolly	32	65.6	1.7*	1.0**	1.0	7.0
<i>CL</i>	Span of years used	Longleaf	66	86.4	4.6*	--	1.0	11.0
		Loblolly	23	73.9	2.6*	2.2**	1.0	8.0
	Total years used	Longleaf	66	86.4	4.6*	--	1.0	10.0
		Loblolly	23	78.9	2.6*	2.2**	1.0	7.0
	Years of continuous use	Longleaf	66	68.2	4.0*	3.0**	1.0	8.0
		Loblolly	23	60.9	4.9*	4.8**	1.0	7.0

* Restricted mean (see Chapter 2)

** 25th percentile

represent real differences between survival curves. Comparison of survival curves was also possible for loblolly pine, although estimation of the mean and median was not. Elimination of unsuitable cavities did not affect duration of continuous use for *FB/MACK* ($z = -0.668$, $p = 0.252$) or for *CNF* ($z = -1.240$, $p = 0.107$). Differences between species were highly significant for *FB/MACK* ($z = 2.298$, $p = 0.011$) but not significant for *CNF* ($z = 0.744$, $p = 0.229$). Statistical tests could not be performed for *CL*. Differences in mean values between cavity populations (Table 4.6) were not significant (extension of Gehan's generalized Wilcoxon test $X^2 = 3.745$, $p = 0.154$).

TABLE 4.4. Statistical test results for comparisons between tree species of duration of use of cavities for roosting (from Table 4.3). Comparisons were conducted using Gehan's generalized Wilcoxon Test.

Cavity population	Measure of use	n	Test statistic (z)	p	Statistical significance
<i>FB/MACK</i>	Span of years	178	3.183	0.001	Y
	Total years	178	3.135	0.001	Y
	Continuous use	178	3.469	0.000	Y
<i>CNF</i>	Span of years	115	2.700	0.003	Y
	Total years	115	2.705	0.003	Y
	Continuous use	115	1.903	0.029	Y
<i>CL</i>	Span of years	89	1.757	0.039	Y
	Total years	89	1.702	0.044	Y
	Continuous use	89	0.273	0.392	N

TABLE 4.5. Statistical test results for comparisons between cavity populations of duration of use of cavities for roosting (from Table 4.3). Comparisons were conducted using a multiple sample test in the Statistica (1993) survival analysis module.

Species	Measure of use	n	Test statistic (X^2)	p	Statistical significance
<i>Longleaf pine</i>	Span of years	312	17.584	0.000	Y
	Total years	312	15.618	0.000	Y
	Continuous use	312	12.118	0.002	Y
<i>Loblolly pine</i>	Span of years	70	1.457	0.483	N
	Total years	70	1.457	0.483	N
	Continuous use	70	1.283	0.527	N

Distributions of duration of use values are reported for both sets of analyses as indicators of the variance inherent in the data (Figure 4.1 and 4.2). These distributions are based exclusively on uncensored observations. As the majority of observations that the analyses are based on are censored (Tables 4.3 and 4.6), these distributions are only partially representative of the true distribution of values. The number of uncensored observations for cavities in loblolly pine was too low to convey any significant information, therefore distributions for cavities in this species are not reported. Likewise, only the distributions of continuous use could be reported for longleaf pine on CNF and CL, and only when lost cavities were included (Figure 4.1). For cavities that remained suitable, only the distribution of continuous use of cavities in longleaf pine on FB/MACK could be shown (Figure 4.2).

TABLE 4.6. Three representative measures of duration in years of use of cavities for roosting. Does not include cavities on trees that died, cavities that broke, cavities that were enlarged or cavities on territories that were abandoned after the cavity was complete.

Cavity population	Measure of use	Species	n	% censored obs.	Mean	Median	Min.	Max.
<i>FB/MACK</i>	Span of years used	Longleaf	114	100.0	--	--	1.0	14.0
		Loblolly	7	100.0	--	--	2.0	9.0
	Total years used	Longleaf	114	100.0	--	--	1.0	14.0
		Loblolly	7	100.0	--	--	2.0	8.0
	Years of continuous use	Longleaf	114	79.8	10.2*	10.3	1.0	14.0
		Loblolly	7	57.1	--	--	2.0	4.0
<i>CNF</i>	Span of years used	Longleaf	50	98.0	--	--	1.0	7.0
		Loblolly	18	100.0	--	--	1.0	7.0
	Total years used	Longleaf	50	98.0	--	--	1.0	7.0
		Loblolly	18	100.0	--	--	1.0	7.0
	Years of continuous use	Longleaf	50	84.0	2.8*	--	1.0	7.0
		Loblolly	18	83.3	--	--	1.0	7.0
<i>CL</i>	Span of years used	Longleaf	45	100.0	--	--	1.0	11.0
		Loblolly	11	100.0	--	--	1.0	8.0
	Total years used	Longleaf	45	100.0	--	--	1.0	10.0
		Loblolly	11	100.0	--	--	1.0	7.0
	Years of continuous use	Longleaf	45	84.4	4.5*	4.3**	1.0	8.0
		Loblolly	11	81.8	--	--	1.0	7.0

* Restricted mean (see Chapter 2)

** 25th percentile

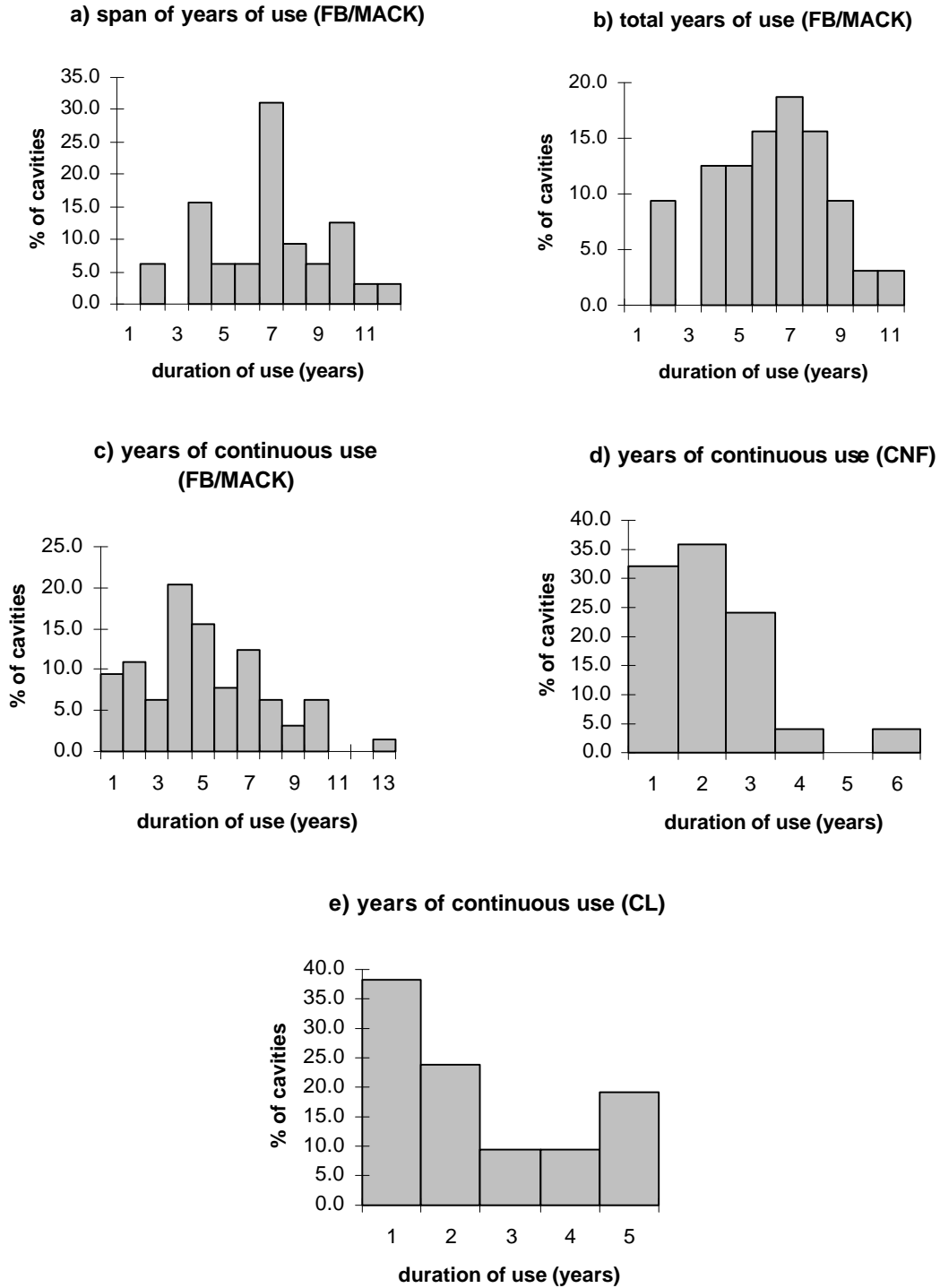


FIGURE 4.1. Percentage distribution of duration of use of cavities in longleaf pine for roosting. Includes only those cavities for which observations of use were not censored. Includes all cavities that were suitable for analysis, regardless of cavity fate. The following measures of use are represented: a) span of years of use on FB/MACK (n = 32), b) total years of use on FB/MACK (n = 32), c) years of continuous use on FB/MACK (n = 64), d) years of continuous use on CNF (n = 25) and e) years of continuous use on CL (n = 21).

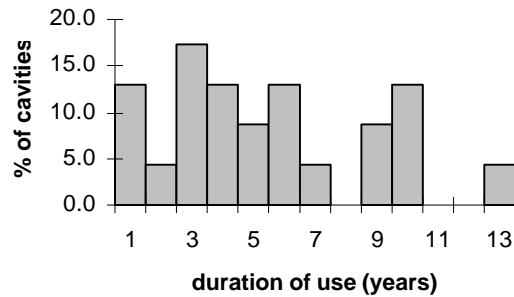


FIGURE 4.2. Percentage distribution of duration of continuous use of cavities in longleaf pine for roosting on FB/MACK. Includes only those cavities for which observations of use were not censored. Does not include cavities on trees that died, cavities that broke, cavities that were enlarged or cavities on territories that were abandoned after the cavity was complete.

TABLE 4.7. Duration in years of continuous use of artificial cavities for roosting. Includes all cavities suitable for analysis regardless of cavity fate.

Cavity population	n	% censored obs.	Mean	Median	Min.	Max.
<i>FB/MACK</i>	26	61.5	3.7*	4.0	1.0	7.0
<i>CNF</i>	21	71.2	2.6*	2.0**	1.0	6.0

* Restricted mean (see Chapter 2)

** 25th percentile

Artificial Cavities

For each of the analyses, the number of uncensored observations within the eligible samples was too small to reliably estimate the survival curves and derive means and medians. The exceptions were the measures of continuous use of cavities in longleaf pine for two of the cavity populations, FB/MACK and CNF. Using the means as estimators of use, cavities were used for 3.7 consecutive years in the Sandhills and 2.6 consecutive years in the coastal population (Table 4.7). Both means were restricted. Significant differences did not exist between artificially and naturally excavated cavities in the latter cavity population ($z = -0.423$, $p = 0.336$), but values were significantly greater for natural cavities on FB/MACK ($z = -2.892$, $p = 0.002$). It is difficult to judge the full potential for the use of artificial cavities based on this information.

Analysis of the Duration of Use of Cavities as Nest Cavities

Naturally Excavated Cavities

Reuse rates of nest cavities are reported in Tables 4.8 and 4.9. Reuse rates could not always be calculated separately for each pine species. For the analyses of use that excluded cavities that did not remain suitable, the sample sizes available for loblolly pine were too small for the calculation of realistic rates. Therefore, a combined rate for longleaf and loblolly pines was

TABLE 4.8. Reuse rates of nest cavities in longleaf and loblolly pine following periods of non-use of various lengths. Includes all cavities suitable for analysis regardless of cavity fate.

Species	<i>FB/MACK</i>			<i>CNF</i>		<i>CL</i>	
	No. years inactive	Sample size	Reuse rate	Sample size	Reuse rate	Sample size	Reuse rate
<i>Longleaf Pine</i>	1	286	0.192	67	0.075	44	0.114
	2	207	0.068	49	0.061	32	0.063
	3	177	0.023	39	0.103	26	0.077
	4	152	0.026	26	0.000	21	0.000
	5	131	0.046	19	0.053	18	0.000
	6	116	0.017	9	0.000	15	0.000
	7	99	0.020	6	0.000	10	0.000
	8	82	0.000	0	--	8	0.000
	9	64	0.016	0	--	5	0.000
	10	50	0.000	0	--	2	0.000
	11	39	0.000	0	--	0	--
	12	29	0.000	0	--	0	--
	13	21	0.000	0	--	0	--
	14	10	0.000	0	--	0	--
<i>Loblolly Pine</i>	1	29	0.345	25	0.200	17	0.118
	2	18	0.000	14	0.071	13	0.000
	3	17	0.059	10	0.000	11	0.000
	4	13	0.000	8	0.125	7	0.000
	5	11	0.000	5	0.000	6	0.000
	6	11	0.000	3	0.000	6	0.000
	7	8	0.000	1	0.000	5	0.000
	8	7	0.000	0	--	3	0.000
	9	7	0.000	0	--	1	0.000
	10	7	0.000	0	--	1	0.000
	11	7	0.000	0	--	0	--
	12	6	0.000	0	--	0	--
	13	3	0.000	0	--	0	--
	14	2	0.000	0	--	0	--

calculated for these analyses (Table 4.9).

Red-cockaded woodpeckers nested in cavities in longleaf pine for a mean of three to four years, three of which were continuous, over the span of three to five years (Table 4.10). The span of use of cavities in loblolly pine was of two to three continuous years (Table 4.10). The range of years over which cavities were used is nearly identical between species in both coastal cavity populations, but is higher in longleaf pine in the Sandhills.

Despite the differences in sample sizes between species, patterns of use of cavities as nests do not appear to differ much between longleaf and loblolly pine. Mean estimates of use are comparable between longleaf and loblolly pine, with the exception of CNF, on which cavities in longleaf pine were used for approximately twice as long (Table 4.10). These were the only

TABLE 4.9. Reuse rates of nest cavities in longleaf and loblolly pine following periods of non-use of various lengths. Does not include cavities on trees that died, cavities that broke, cavities that were enlarged or cavities on territories that were abandoned after the cavity was complete. Combined reuse rates were calculated for longleaf and loblolly pine for CNF and for CL.

No. years inactive	<i>FB/MACK (longleaf)</i>		<i>FB/MACK (loblolly)</i>		<i>CNF</i>		<i>CL</i>	
	Sample size	Reuse rate	Sample size	Reuse rate	Sample size	Reuse rate	Sample size	Reuse rate
1	195	0.241	18	0.500	40	0.200	29	0.172
2	132	0.091	9	0.000	24	0.167	17	0.059
3	107	0.037	8	0.125	12	0.083	13	0.154
4	92	0.011	6	0.000	10	0.100	9	0.000
5	81	0.062	6	0.000	6	0.000	8	0.000
6	71	0.014	6	0.000	4	0.000	6	0.000
7	63	0.032	3	0.000	1	0.000	4	0.000
8	50	0.000	3	0.000	0	--	2	0.000
9	41	0.024	2	0.000	0	--	2	0.000
10	33	0.000	2	0.000	0	--	2	0.000
11	27	0.000	2	0.000	0	--	0	--
12	21	0.000	1	0.000	0	--	0	--
13	15	0.000	1	0.000	0	--	0	--
14	7	0.000	1	0.000	0	--	0	--

significant differences, although differences in the span of years of use on FB/MACK approached significance (Table 4.11).

Mean estimates of duration of cavity use did not vary much between populations, although the estimates tended to be highest in the Sandhills and lowest on CNF (Table 4.10) for both pine species. No differences were significant (Table 4.12).

Limiting the analyses to ideal conditions (i.e. cavities that remain suitable) had a noticeable effect on duration of cavity use in longleaf pine, but not in loblolly. On FB/MACK, cavities that remained suitable in longleaf pine were used for a mean of 4.5 years over a span of 5.7 years, and were used continuously for nearly three years (Table 4.13). This represents a moderate increase over the previous analysis in the first two measures of use, and these differences were significant (Table 4.14). Although the number of uncensored observations in the analyses for CNF allowed estimation of parameters only for continuous use (Table 4.13), the curves representing total use and span of years of use indicated greater use of cavities that remained suitable (Table 4.14). Differences were not significant on CL, however (Table 4.14), for which the estimated means of each of the measures of use were slightly lower when unsuitable cavities were excluded (Table 4.13). This decrease is probably due to the distribution of censored observations in the sample, of which there were more in these analyses.

The number of uncensored observations in the analyses of loblolly pine again permitted estimation of only continuous use on CNF, and precluded estimation of all measures of use on CL. Mean total use and span of use of cavities as nests in loblolly pine was 2.5 years on

TABLE 4.10. Three representative measures of duration in years of use of cavities as nests. Includes all cavities suitable for analysis regardless of cavity fate.

Cavity population	Measure of use	Species	n	% censored obs.	Mean	Median	Min.	Max.
<i>FB/MACK</i>	Span of years used	Longleaf	186	33.9	4.6*	4.0	1.0	13.0
		Loblolly	18	16.7	3.3*	2.9	1.0	8.0
	Total years used	Longleaf	186	33.9	3.8	3.0	1.0	9.0
		Loblolly	18	16.7	3.3	2.9	1.0	7.0
	Years of continuous use	Longleaf	186	17.2	2.7*	2.0	1.0	7.0
		Loblolly	18	11.1	2.9	2.0	1.0	7.0
<i>CNF</i>	Span of years used	Longleaf	33	63.6	3.2*	3.8	1.0	7.0
		Loblolly	12	41.7	1.7*	1.7	1.0	7.0
	Total years used	Longleaf	33	63.6	3.1*	3.2	1.0	6.0
		Loblolly	12	41.7	1.6*	1.7	1.0	6.0
	Years of continuous use	Longleaf	33	45.5	2.7*	2.0	1.0	5.0
		Loblolly	12	25.0	2.2	1.6	1.0	4.0
<i>CL</i>	Span of years used	Longleaf	29	48.3	3.5*	3.9	1.0	7.0
		Loblolly	8	12.5	3.1	2.0	1.0	6.0
	Total years used	Longleaf	29	48.3	3.5*	3.9	1.0	6.0
		Loblolly	8	12.5	3.1	2.0	1.0	6.0
	Years of continuous use	Longleaf	29	37.9	3.2*	3.0	1.0	6.0
		Loblolly	8	12.5	3.1	2.0	1.0	6.0

* Restricted mean (see Chapter 2)

TABLE 4.11. Statistical test results for comparisons between tree species of duration of use of cavities as nest cavities (from Table 4.10). Comparisons were conducted using Gehan's generalized Wilcoxon Test.

Cavity population	Measure of use	n	Test statistic (z)	p	Statistical significance
<i>FB/MACK</i>	Span of years	204	1.426	0.077	N
	Total years	204	0.924	0.178	N
	Continuous use	204	- 0.467	0.320	N
<i>CNF</i>	Span of years	45	2.118	0.017	Y
	Total years	45	2.147	0.016	Y
	Continuous use	45	1.032	0.151	N
<i>CL</i>	Span of years	37	1.004	0.158	N
	Total years	37	0.963	0.168	N
	Continuous use	37	0.655	0.256	N

TABLE 4.12. Statistical test results for comparisons between cavity populations of duration of use of cavities as nest cavities (from Table 4.10). Comparisons were conducted using a multiple sample test in the Statistica (1993) survival analysis module.

Species	Measure of use	n	Test statistic (X^2)	p	Statistical significance
<i>Longleaf pine</i>	Span of years	98	0.309	0.857	N
	Total years	98	0.896	0.639	N
	Continuous use	98	4.411	0.110	N
<i>Loblolly pine</i>	Span of years	38	0.728	0.695	N
	Total years	38	0.802	0.670	N
	Continuous use	38	1.020	0.601	N

TABLE 4.13. Three representative measures of duration in years of use of cavities as nests. Does not include cavities on trees that died, cavities that broke, cavities that were enlarged or cavities on territories that were abandoned after the cavity was complete.

Cavity population	Measure of use	Species	n	% censored obs.	Mean	Median	Min.	Max.
<i>FB/MACK</i>	Span of years used	Longleaf	123	48.0	5.7	5.0	1.0	13.0
		Loblolly	8	37.5	2.5*	2.8	1.0	8.0
	Total years used	Longleaf	123	48.0	4.5	4.0	1.0	9.0
		Loblolly	8	37.5	2.5*	2.8	1.0	4.0
	Years of continuous use	Longleaf	123	23.6	2.7*	2.0	1.0	7.0
		Loblolly	8	25.0	1.8*	2.0	1.0	3.0
<i>CNF</i>	Span of years used	Longleaf	17	82.4	--	--	1.0	7.0
		Loblolly	7	71.4	--	--	1.0	7.0
	Total years used	Longleaf	17	82.4	--	--	1.0	6.0
		Loblolly	7	71.4	--	--	1.0	6.0
	Years of continuous use	Longleaf	17	47.1	2.8	2.7	1.0	5.0
		Loblolly	7	42.9	2.7	1.4	1.0	4.0
<i>CL</i>	Span of years used	Longleaf	21	61.9	3.3*	4.0	1.0	7.0
		Loblolly	4	50.0	--	--	1.0	6.0
	Total years used	Longleaf	21	61.9	3.3*	4.0	1.0	6.0
		Loblolly	4	50.0	--	--	1.0	6.0
	Years of continuous use	Longleaf	21	42.9	3.1*	3.0	1.0	6.0
		Loblolly	4	25.0	--	--	1.0	6.0

*Restricted mean (see Chapter 2)

FB/MACK, and continuous use ranged from 1.8 to 2.7 years among cavity populations (Table 4.13). These values represent a slight increase in continuous use on CNF from the values of the analyses that include all cavities, and a decrease for all three measures of use on FB/MACK (Tables 4.10 and 4.13). The survival curves associated with use values on FB/MACK shifted to the right for the span of years of cavity use, but to the left for the remaining measures of use. None of the differences between the two analyses were significant (Table 4.14). Differences between pine species within the analysis that excluded cavities that became unsuitable likewise were not significant for the tests that could be performed (Table 4.15).

TABLE 4.14. Test results for comparisons of duration of use of cavities as nest cavities between all cavities (from Table 4.10) and cavities that remained suitable (from Table 4.13). Comparisons were conducted using Gehan's generalized Wilcoxon Test.

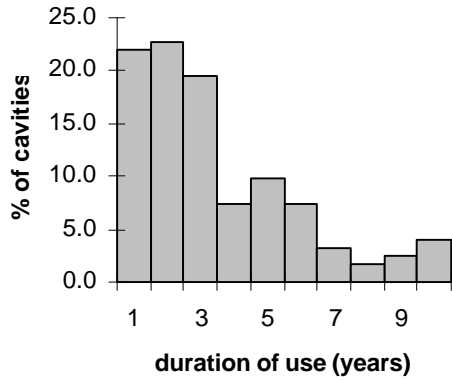
Species	Cavity population	Measure of use	n	Test statistic (z)	p	Statistical significance
<i>Longleaf pine</i>	FB/MACK	Span of years	309	- 1.744	0.040	Y
		Total years	309	- 1.894	0.029	Y
		Continuous use	309	- 0.429	0.334	N
	CNF	Span of years	50	- 1.888	0.030	Y
		Total years	50	- 1.876	0.030	Y
		Continuous use	50	- 0.278	0.391	N
	CL	Span of years	50	- 0.832	0.202	N
		Total years	50	- 0.832	0.202	N
		Continuous use	50	- 0.404	0.343	N
<i>Loblolly pine</i>	FB/MACK	Span of years	26	- 0.339	0.367	N
		Total years	26	- 0.280	0.390	N
		Continuous use	26	0.117	0.453	N
	CNF	Continuous use	19	- 0.024	0.490	N
		CL	Continuous use	12	- 0.720	0.236

TABLE 4.15. Statistical test results for comparisons between tree species of duration of use of cavities as nest cavities for cavities that remained suitable (from Table 4.13). Comparisons were conducted using Gehan's generalized Wilcoxon Test.

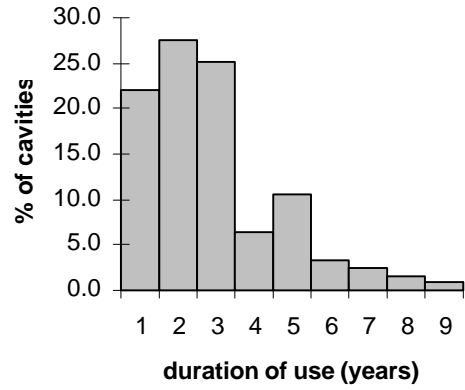
Cavity population	Measure of use	n	Test statistic (z)	p	Statistical significance
<i>FB/MACK</i>	Span of years	131	1.071	0.142	N
	Total years	131	0.877	0.190	N
	Continuous use	131	- 0.056	0.478	N
<i>CNF</i>	Continuous use	24	0.817	0.207	N
<i>CL</i>	Continuous use	25	0.000	0.500	N

Distributions are again reported for both sets of analyses (Figures 4.3 - 4.5). Because of sample sizes of uncensored observations, not all distributions could be shown. For the analyses based on all cavities, uncensored observations constituted the majority of observations for FB/MACK, but only half of the observations for CL (Table 4.10). The distributions, which are based on uncensored observations only, should thus be interpreted with caution in the latter case. Similarly, for the analyses based exclusively on cavities that remain suitable, approximately half

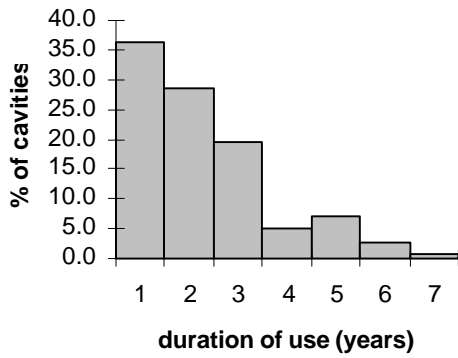
a) span of years of use (FB/MACK)



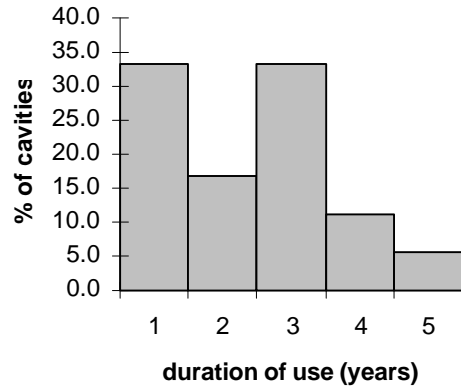
b) total years of use (FB/MACK)



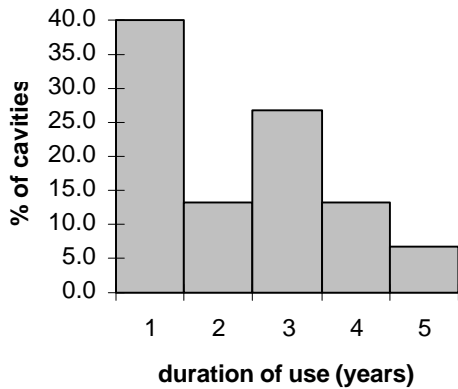
c) years of continuous use (FB/MACK)



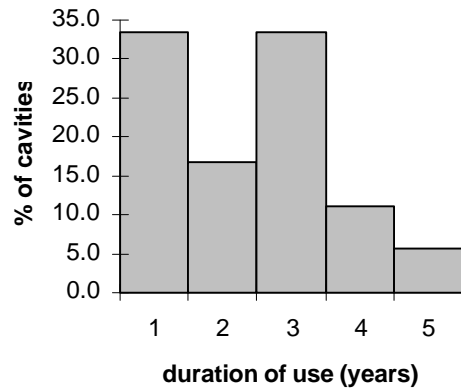
d) span of years of use (CL)



e) total years of use (CL)



f) years of continuous use (CL)



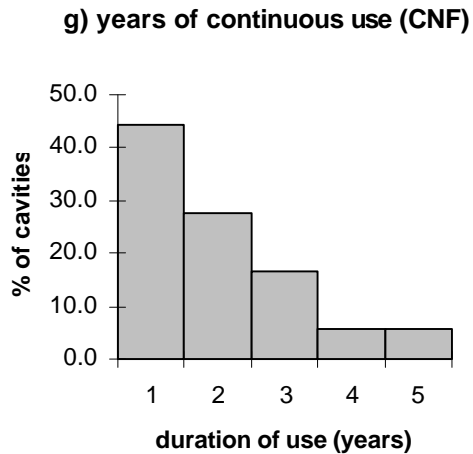


FIGURE 4.3. Percentage distribution of duration of use of cavities in longleaf pine for nesting. Includes only those cavities for which observations of use were not censored. Includes all cavities that were suitable for analysis, regardless of cavity fate. The following measures of use are represented: a) span of years of use on FB/MACK (n = 123), b) total years of use on FB/MACK (n = 123), c) years of continuous use on FB/MACK (n = 154), d) span of years of use on CL (n = 15), e) total years of use on CL (n = 15), f) years of continuous use on CL (n = 18) and g) years of continuous use on CNF (n = 18).

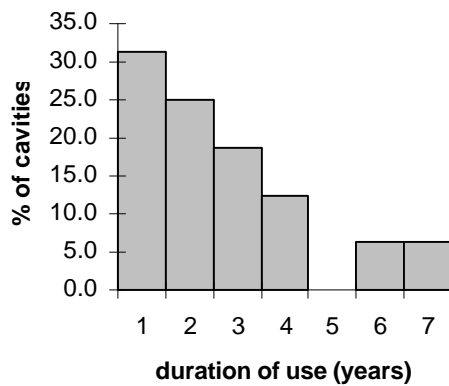


FIGURE 4.4. Percentage distribution of duration of continuous use of cavities in loblolly pine for nesting on FB/MACK. Includes only those cavities for which observations of use were not censored (n = 16). Includes all cavities that were suitable for analysis, regardless of cavity fate.

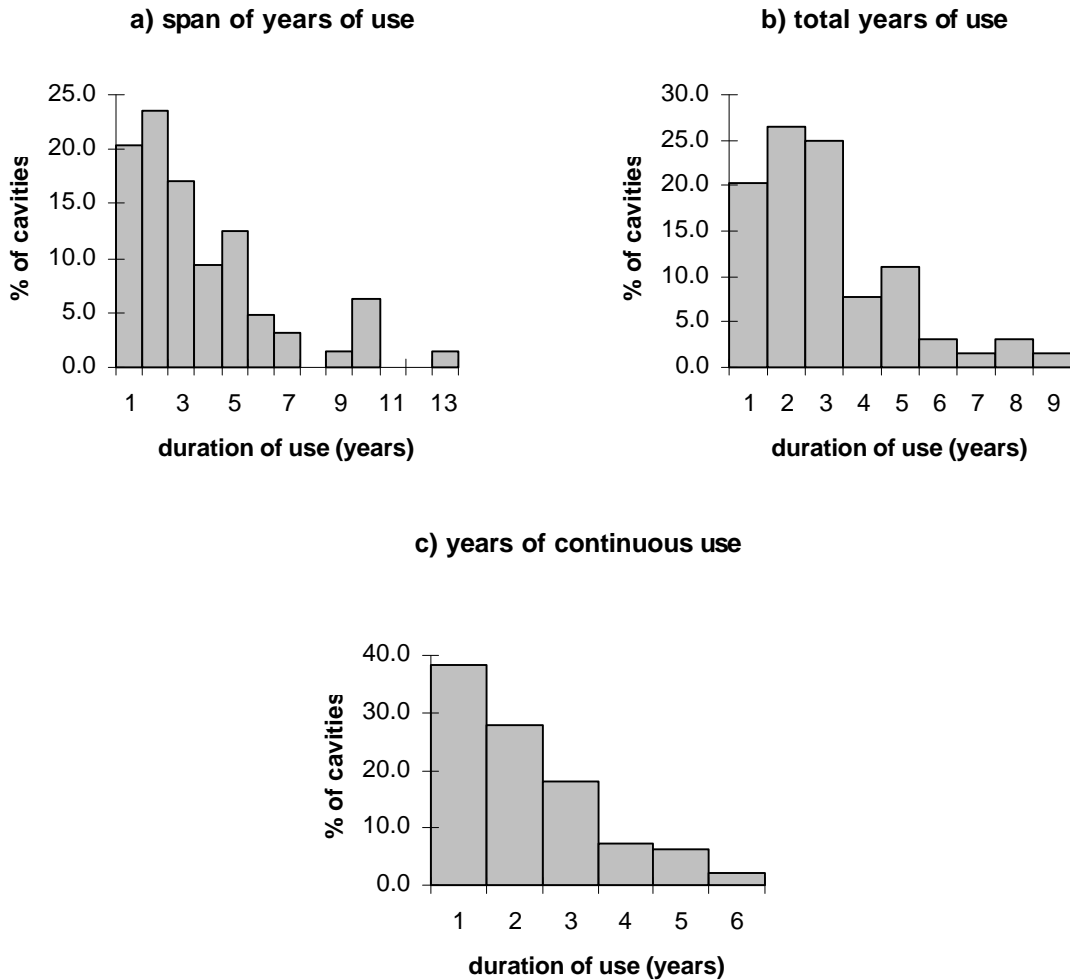


FIGURE 4.5. Percentage distribution of duration of use of cavities in longleaf pine for nesting on FB/MACK. Includes only those cavities for which observations of use were not censored. Does not include cavities on trees that died, cavities that broke, cavities that were enlarged or cavities on territories that were abandoned after the cavity was complete. The following measures of use are represented: a) span of years of use (n = 64), b) total years of use (n = 64) and c) years of continuous use (n = 94).

of the observations were uncensored (Table 4.13).

Artificial Cavities

Of 102 artificial cavities constructed on FB, 23 were used as nest cavities for one or more years between 1989 and 1995, as were two of seven constructed on Camp Mackall. On CNF, 11 artificial cavities of 150 constructed were used as nests between 1992 and 1996, and on CL, 15 of 63 were used between 1993 and 1996. Based on the established criteria, the number of cavities suitable for analysis was too low to conduct meaningful analyses for loblolly pine (three or less). The number of uncensored observations likewise precluded analysis of longleaf pine for CL and of all measures of use except continuous use for CNF. For the analyses that were conducted, results

for longleaf pine (Table 4.16) were comparable to results for natural cavities (Table 4.10). It is interesting that, although the maximum values for artificial cavities were considerably lower than those for naturally excavated cavities, artificial cavities were used as nests for a significantly greater number of continuous years (Table 4.17). It appears that artificial cavities have value as nest sites comparable to that of natural cavities.

TABLE 4.16. Duration (in years) of use of artificial cavities as nests in longleaf pine by red-cockaded woodpeckers. Includes all cavities regardless of fate.

Cavity population	Measure of use	n	% censored obs.	Mean	Median	Min.	Max.
<i>FB/MACK</i>	Span of years	21	71.4	3.8	4.0	1.0	5.0
	Total years	21	71.4	3.8	4.0	1.0	5.0
	Continuous use	21	66.7	3.7	4.0	1.0	5.0
<i>CNF</i>	Continuous use	10	40.0	2.1	2.0	1.0	3.0

TABLE 4.17. Test results for comparisons of duration of use of cavities as nest cavities between naturally excavated cavities (from Table 4.10) and artificial cavities (from Table 4.16).

Cavity population	Measure of use	n	Test statistic (z)	p	Statistical significance
<i>FB/MACK</i>	Span of years	207	0.751	0.226	N
	Total years	207	1.100	0.136	N
	Continuous use	207	2.225	0.013	Y
<i>CNF</i>	Continuous use	43	0.409	0.341	N

Discussion

Patterns of Cavity Use

Although the process of cavity excavation is lengthy (see Chapter 3), cavities, once completed, are used by red-cockaded woodpeckers for periods of years which may exceed the 12 year lifespan (Jackson 1994) of an individual woodpecker (Lay and Russel 1970). Conner and Rudolph's (1995a) study on woodpeckers in Texas estimated that cavities in longleaf pine were used for a total of 8.7 years, 3.1 of them as nests, over a span of 10.3 years. The woodpeckers used cavities in loblolly for 4.8 years, 1.8 of them as nests, over a span of 5.2 years. My findings corroborate these results: depending on the cavity population, cavities in longleaf pine were used for five to nine years, three to four of them as nests, while cavities in loblolly pine were used for two to four years, two to three of them as nests. My estimates are lower than those of Conner and Rudolph (1995a), but mine are certainly underestimates. The fact that the distribution of

cavity use values did not permit calculation of medians suggests that duration of use of individual cavities in longleaf pine far exceeds the duration of the longest record in my study. Longleaf cavities that had remained active for 14 years were in fact still being used (Table 4.3).

The cycle of cavity use begins upon completion of excavation. Although the vast majority of cavities are used for roosting in the first breeding season following their completion (Table 4.18), use of a cavity as a nest may be delayed for as many as six years following cavity completion, and in one case in longleaf pine began nine years following completion (Table 4.19). It is likely that these particular cavities are used as nests for short periods in the absence of preferred cavities.

A substantial proportion of cavities (approximately 40 %) are not used as nests immediately following completion (Table 4.19). This occurs for three reasons: (1) no reproductive attempt was made in that year (36.7 % of cases, n = 120); (2) more than one cavity was completed simultaneously, so that another newly excavated cavity was used as a nest (5.0 % of cases); or (3) an already excavated cavity was used as a nest (58.3 % of cases). The last scenario explains the majority of the instances in which a newly completed cavity was not used as a nest in the year in which a group nested. This suggests that the need for nest cavities is not a major factor influencing excavation.

TABLE 4.18. Number of cavities used for roosting following periods of various lengths representing the number of years between cavity completion and first use. Includes cavities on FB/MACK, CNF and CL (from Table 4.3).

Number of years	Longleaf pine	Loblolly pine	Pond pine	Total
0	302	69	6	377
1	7	0	0	7
2	3	1	1	5
3	1	0	0	1

TABLE 4.19. Number of cavities used for nesting following periods of various lengths representing the number of years between cavity completion and first use. Includes cavities on FB/MACK, CNF and CL (from Table 4.10).

Number of years	Longleaf pine	Loblolly pine	Pond pine	Total
0	147	22	3	172
1	50	11	1	62
2	25	2	0	27
3	13	3	0	16
4	5	0	1	6
5	4	0	1	5
6	3	0	0	3
7	0	0	0	0
8	0	0	0	0
9	1	0	0	1

Of the cavities used as nests, the majority that are not used immediately are used within three years of completion (over half of them after one year). It is clear then that newer cavities are preferred over older cavities as nests. Conner et al. (in press) suggested that use of new cavities may help reduce parasite loads for both nestlings and incubating adults. They found that red-cockaded woodpeckers in Texas tend to select the newest cavity for nesting when only naturally excavated cavities are available. However, when both natural and artificial cavities are present, the newest cavity was selected in less than half of all cases (Conner et al., in press), suggesting that patterns of nest cavity selection are disrupted by the presence of artificial cavities. This could explain why the newest cavity was not always used as the nest cavity in my study. However, as it is unlikely that artificial cavities were present in all instances in which the newest cavity was not selected in my study, my results do not completely corroborate those of Conner et al. (in press).

It is unknown whether older cavities are used as nests for a shorter duration of time than newer cavities. However, it appears from the similarity between estimates of continuous use and the other measures of use (Table 4.10), as well as from the reuse rates (Table 4.8), that once cavities cease being used as nests they tend not to be used as nests again. Although the majority of cavities are abandoned as nests following periods of inactivity as short as one year (Tables 4.8 and 4.9), a small number of cavities are nested in after as many as nine years of inactivity in longleaf pine and four years in loblolly. The use of these older cavities as nests may again be explained by the loss of preferred cavities.

Not all cavities are used as nests, but nearly all are roosted in. Approximately seven percent ($n = 419$) of cavities had not yet been used as roosts or nests before the end of each study, however. Approximately half of these cavities broke from a tree, were on a tree that died, or were enlarged within three years of having been completed. The other half, however, appeared to be suitable throughout the study period. Each of these had not been used for three years or less before the study period ended. It is unclear why some suitable cavities are not used immediately upon completion, especially given that cavities can be completed after sitting idle as non-completed cavities for several years (see Chapter 3). Because these suitable cavities are in the minority, however, it is likely that the lack of use of each is the result of a particular set of circumstances unique to that cavity.

Cavities are used for roosting longer than they are used for nesting, indicating that a cavity that is no longer used as a nest continues to be roosted in for periods that may exceed 14 years in longleaf pine and ten years in loblolly. Cavities that are used as nests are typically roosted in by the breeding male of a group (Ligon 1970, Jackson 1994). Once the male switches to a newer cavity for both nesting and roosting, the vacated cavity may be occupied by another group member (Walters, pers. comm.). Use of an individual cavity may thus involve occupancy by more than one woodpecker over the cavity's lifespan, as the cavity is alternately vacated and reoccupied by various members of a group (Walters, pers. comm.). Although cavities have a greater probability of being reused as roosts than as nests following suspension of use, less than one half of all cavities that are not used for one year are roosted in again (Tables 4.1 and 4.2). This, along with the close correspondence between the three measures of use (Table 4.3), indicates that initial vacancy often signifies final abandonment, although cavities may be used intermittently. Intermittent use may be a function of the number of woodpeckers in a group. Due to the

dynamics of dispersal and of competition for breeding vacancies in neighboring territories (Walters 1990, Walters et al. 1988), group size is variable between years. Therefore, cavities that would otherwise be occupied may be vacant in certain years because there may not be a sufficient number of individuals in a group to occupy all suitable cavities in a cluster. Final abandonment of a cavity, however, appears to be related to the action of forces that render the cavity unsuitable for use. In fact, no cavity in either longleaf or loblolly pine completed during the study that was not lost to external factors was permanently abandoned (Table 4.6). These issues are explored further in the next section.

Differences in Duration of Use Between Tree Species

Duration of use of cavities excavated in longleaf pine doubled and even tripled that of cavities in loblolly pine. That such differences exist between pine species suggests that different species may be of different value to the woodpecker. However, the tree with the most potential as a cavity tree is the one for which the ratio of use time to excavation time is the greatest. The ratio of cavity use (span of years of use as roost cavities) to excavation is calculated using mean estimates of excavation length that include censored observations. On FB/MACK, this ratio is 0.6 and 0.9 for longleaf and loblolly pine, respectively, while on both CNF and CL it is 0.5 and 0.3 for longleaf and loblolly pine, respectively. The ratio for loblolly pine on FB/MACK is overestimated because the estimate of excavation length does not include excavation from substart to start. If excavation of this stage transition were assumed to require one year (based on values for the other populations), the ratio would be closer to 0.7. The ratios are therefore either higher in longleaf pine or similar between species, suggesting that the potential of longleaf as cavity trees is somewhat higher. These results are quite different from those reported by Conner and Rudolph (1995a), who found greater differences in duration of excavation and smaller differences in duration of use between pine species. Based on their published estimates, the ratio of cavity use to excavation is 1.6 years for longleaf pine and 2.9 for loblolly, suggesting that loblolly pine is the superior species. What is abundantly clear from both their results and my results is that excavating in longleaf is more difficult, but that longleaf cavities, once completed, are more valuable than those in loblolly.

It is interesting that the length of use of cavities in the two tree species differs for roosting, but not for nesting. This is contrary to what Conner and Rudolph (1995a) found in Texas, where cavities in longleaf were used as nests for nearly twice as long as cavities in loblolly. Although differences between species were not detected on FB/MACK and CL, they did exist on CNF, where nests in longleaf were used twice as long. The significance of these results is unclear. However, it appears that, in general, cavities in loblolly pine are used as nests almost until final abandonment (Tables 4.3 and 4.10), whereas, as discussed in the previous section, cavities in longleaf are still roosted in after they are no longer used as nests. Differences in a cavity's suitability for each of the two activities appear to be related to a tree's potential for sap production, as nest cavities in longleaf pine are located in trees that are better resin producers than those trees used for roosting (Conner et al., in press).

It was found that cavities excavated in longleaf pine were used as nests for moderately longer periods of time under ideal conditions (i.e. when the cavities were not lost to tree death or cavity

enlargement). This suggests that tree death and cavity enlargement have an effect on use of nest cavities in longleaf, but that this effect is minor. The same can not be said for loblolly cavities, which appear to realize their full use potential and become abandoned prior to cavity loss. Given this result, it is expected that differences should exist between the two species in cavity use under ideal conditions, that is, in unrealized use potential. That such an effect could not be demonstrated is likely the result of low sample sizes for loblolly pine. Also potentially confounding the effects of enlargement and tree death on nest cavity use is cluster abandonment by the woodpeckers, as completed cavities on abandoned clusters were excluded from the analyses of use under ideal conditions. Although it certainly leads to suspension of use of a cavity, cluster abandonment may be a response to cavity unsuitability in the first place.

Examination of the unrealized use potential of cavities for roosting yielded results that are difficult to interpret, as the analyses could be conducted only for duration of continuous use. Although differences were found between unrealized and realized use potential for each pine species, it is unclear whether cavities that remain suitable are used for longer periods of time than unsuitable cavities. It is possible that there is merely a difference in the patterns of continuous use over the same span of years between suitable and unsuitable cavities. Under this scenario, enlarged cavities may be used intermittently by red-cockaded woodpeckers when higher quality cavities are not available, whereas cavities that are not enlarged are used for longer continuous periods.

Cavities in longleaf pine are used as roosts for longer periods than are cavities in loblolly pine. It is interesting that patterns of cavity use, as defined by differences and similarities between the measures of use, do not differ between the tree species. The ratio of total use to span of use is virtually identical between the two species (Table 4.3) and rates of reuse are likewise comparable between them (Table 4.1). Differences between tree species thus appear to be related exclusively to duration of use, rather than to patterns of use during the period that a cavity is used. One possible explanation of these interspecific differences in duration is that loblolly suffer more from various factors that cause cavities to be lost, such as enlargement by other cavity-dwelling species, tree death, encroachment of hardwood midstory and fungal rot. As discussed above, unequivocal tests of differences between realized and unrealized use were not possible for those factors considered in the analyses (cavity enlargement and tree death), and other factors (hardwood encroachment and fungal rot) were not considered. However, loblolly cavities appear to be more susceptible to loss than longleaf cavities. The percentage of suitable cavities lost within each species was consistently greater for loblolly cavities across all cavity populations, although the magnitude of this difference varied (see Chapter 5). The greater losses of cavities in loblolly may in part be due to the fact that loblolly has softer wood (Carter, pers. comm.) and may be more vulnerable to cavity enlargement as a result.

Cavity loss thus may be operating differentially between pine species, in the process leading to differences in duration of use. Cavity loss is unlikely to be the only factor involved, however. One hypothesis is that differences between pine species are the result of differences in their ability to produce sap. Strong sap flow provides an effective defense against predating rat snakes (Jackson 1974, Rudolph et al. 1990a). Longleaf pine is capable of producing greater amounts of resin and of sustaining sap flow for lengthier periods of time than is loblolly (Hodges et al. 1977

and 1979, Hicks 1980). The hypothesis assumes that the birds can assess the effectiveness of the resin barrier they create around their cavities. This assumption is consistent with the bird's well documented tendency to abandon cavities on which hardwoods encroach (Locke et al. 1983, Hovis and Labisky 1985, Conner and Rudolph 1991, Loeb et al. 1992). Encroachment of hardwoods surrounding a cavity tree allows predators to gain access to a cavity by crossing on branches above the cavity.

Differences in Duration of Use Between Cavity Populations

Duration of red-cockaded woodpecker use of cavities excavated in loblolly pine did not appear to vary among cavity populations, but duration of use of cavities in longleaf pine did. Interestingly, duration of use of cavities in longleaf was longer in the Sandhills, where excavation times were also longer, and was similar between the coastal populations, where excavation times were also similar. This suggests that cavity excavation and use are affected by a common set of factors that vary between geographical areas. Such factors could be intrinsic to the cavity tree, relating to its physical characteristics, or could operate externally to both cavity and tree.

The most obvious factor to simultaneously affect excavation and use of cavities is the strength of a tree's sap flow. Strong sap flow could result in lengthier excavation, as discussed in the previous chapter, and subsequently prolong use of a cavity, as discussed above. It was concluded in the preceding chapter, however, that differences in sap flow offer an unlikely explanation for differences in duration of excavation. Furthermore, it is difficult to conceive that strength of sap flow within a tree species would vary between study areas to such an extent as to produce the differences in cavity use seen here. Finally, the conditions that cause differences between longleaf pine in different areas would be expected to affect loblolly pine in the same way. It is therefore unlikely that this particular physical characteristic of trees can be linked to variation in use and excavation of cavities among cavity populations. Factors external to cavities and to cavity trees are more likely implicated.

As discussed in Chapter 3, infection of a tree by red heart fungus can contribute to shorter excavation times by facilitating excavation through the heartwood (Jackson 1977b, Conner and Locke 1982, Hooper 1988, Hooper et al. 1991, Rudolph et al. 1995). However, rot concurrent or subsequent to fungal invasion of heartwood may damage sapwood and kill infected trees (Conner et al. 1976). Red heart fungus itself can also shorten the lifespan of trees (Hepting 1971, cited in Jackson 1977b), thus rendering cavities unusable through tree loss. If the same processes affecting duration of excavation can affect the lifespan of pine trees, then differences between cavity populations could be due to differences in infection rates. As an external agent, it is conceivable that fungi could differ in abundance and distribution between cavity populations. The data do not support this hypothesis, however, as fungal infection does not appear to be a major cause of tree mortality in any of the cavity populations in this study (see Chapter 5).

Loss of cavities to other factors may play a role in variation of duration of use and of excavation. The percentage of cavities in longleaf that were lost to tree death and cavity enlargement over the course of each study period (see Chapter 5) was lower in the Sandhills (51.9 %) than on either CNF (60.2 %) or CL (67.5 %). That losses were lower in the Sandhills

suggests that cavity loss may be having a greater effect on cavity use in the coastal populations, where duration of use is in fact lower, than in the Sandhills, where duration of use is greater. The percentages of losses of cavities excavated in loblolly pine, on the other hand, did not differ between cavity populations (see Chapter 5). The absence of differences is consistent with the fact that no differences in duration of cavity use were found between populations for loblolly. In addition, no differences existed between populations in the potential for use of cavities in longleaf pine under ideal conditions, further suggesting that duration of use in longleaf is affected by cavity loss. Because the comparison between populations in unrealized use potential was based on the least telling of the measures of use (i.e. duration of continuous use), the results of the comparison are open to interpretation. As discussed in the previous chapter, cavity loss may indirectly affect duration of cavity excavation through an increased excavation response to the need for new cavities. Variation in cavity loss between cavity populations may thus at least partially explain variation in cavity excavation and use, but more direct evidence of the effect of loss is needed in order to make a conclusive statement.

An alternative to the explanations suggested so far lies with the size of the woodpecker populations and their distribution among clusters. As discussed previously (see Chapter 3), effort on the part of the woodpeckers likely accounts for much of the variation in duration of excavation that is prevalent within the cavity populations. Effort in turn may be a function of the number of birds in a cluster in relation to the number of available cavities (this issue is explored further in Part II (Chapter 6) of this thesis). It is possible that the dynamics of cavity use may be affected by bird to cavity ratios in a similar manner. Differences in ratios between study areas may thus help account for differences in both the use and excavation of cavities. Likewise, the availability of trees suitable for excavation may be affecting duration of cavity use in that cavities may be used longer in areas where suitable trees are scarce (although excavation of multiple cavities in the same tree in the study populations is not uncommon).

Artificial Cavities

The use of artificial cavities to reduce abandonment of territories by supplementing naturally excavated cavities has become an increasingly popular management tool (Walters et al. 1995b). Artificial cavities also have been used to induce formation of new woodpecker groups on unoccupied habitat (Walters et al. 1992b, Copeyon et al. 1991) and thus to stimulate population expansion (Walters et al. 1995b). Artificial cavities are used for both roosting and nesting by the woodpeckers, who will even complete excavation on cavities drilled to the advanced start stage (see Chapter 5). In assessing the utility of artificial cavities, however, it is important to know not only that the birds will use them, but to know to what extent they will use them. In the Sandhills, artificial cavities have amply demonstrated their value as nests, but their value as roost cavities is still undetermined. Duration of use of cavities as nests was comparable between artificial and natural cavities, and artificial cavities were actually used for a greater number of consecutive years. Results were equivocal in relation to the use of cavities for roosting, however. In the Sandhills, duration of continuous use of artificial cavities as roosts was similar to their use as nests and was less than half of the duration of continuous use for naturally excavated cavities. Although these results may have implications for the total number of years that artificial cavities

are used, they may simply indicate that artificial cavities are used more intermittently than are naturally excavated cavities.

Some artificial cavities were used for the entire span of years that they were available to the woodpeckers. This is encouraging, as it shows that artificial cavities do have the potential to be used for long periods of time. As knowledge of the total duration of use and of the span of use are critical for an assessment of the value of artificial cavities to red-cockaded woodpeckers, more data are necessary to permit the use of survival analysis for the estimation of these measures.

Chapter 5: Cavity Turnover

Methods

Cavity Turnover

The turnover of naturally excavated, completed red-cockaded woodpecker cavities was measured for each of the four cavity populations in the study (MACK, FB, CNF and CL). Turnover is expressed as the difference between cavity gains and losses, which were calculated using the woodpecker's breeding season as a point of reference marking the year in which gains and losses occurred. Gains and losses of cavities were quantified for FB and MACK between the years 1980 and 1995, for CNF between the years 1988 and 1996, and for CL between the years 1986 and 1996. Monitoring of the cavity population on CL actually began during the post-breeding season of 1985, but only 28 of the 39 clusters updated in 1986 were visited. Gains and losses were therefore calculated from 1986 onward for this cavity population. Completed cavities that were suitable (i.e. not already lost; see definition of loss below) and that were already in existence during the first year of a study for a cavity population comprise what is referred to as the baseline cavity population. In addition to the clusters updated in the first year of each study, some clusters were updated for the first time in the years following. On FB, 29 such clusters were updated for the first time between 1981 and 1992, while on MACK, two clusters were first visited in 1985. On CNF, 16 clusters were first visited between 1989 and 1995, and on CL, 9 clusters were first updated between 1987 and 1996. Those suitable, completed cavities found in these clusters in the particular years in which they were first visited were added to the baseline cavity population in those years. Although they were not included among the gains, the cavities were incorporated in the calculation of the yearly number of suitable cavities.

Losses attributed to the July and September storms that struck the coast of North Carolina in 1996 were not tabulated in these analyses, as (1) the losses occurred during the post-breeding season of the last year of the studies on CL and CNF and (2) the losses do not represent general trends attributable to natural processes (see below) acting over a relatively long temporal scale. Rather, the losses are the product of a localized natural event of brief duration and of infrequent occurrence (i.e. catastrophic events).

Cavity Gains

Cavity gains were calculated based on two categorizations of completed cavities: cavities that are newly excavated by red-cockaded woodpeckers and cavities that are newly discovered. The former category consists of (1) completed cavities for which data were recorded when the cavities were not yet completed, and (2) cavities which were judged to have been recently completed during field updating. The remaining cavities, for which data preceding completion are not available, were categorized as newly discovered cavities. Newly discovered cavities that were suitable for red-cockaded woodpecker use were incorporated into the calculation of gains for the year in which data on those cavities were first recorded. The percentage of newly discovered cavities contributing to the gains in each year are reported in Table 5.1.

A system was devised to estimate the year of completion of newly excavated cavities when data from the preceding year(s) were missing. If a cavity was judged as having been recently completed, the cavity was assumed to have been completed in the year of the update. For the remaining cavities, completion was estimated as having occurred halfway through the period during which the cavities were not updated. If this period consisted of an even number of years, a coin toss was used to determine on which side of the halfway point the cavity was completed. The accuracy of estimation under this system suffers proportionately to the length of time that a cavity was not updated.

Cavity gains are reported both as absolute numbers and as rates. Both were compared between tree species and examined for all species combined. Yearly rates of gain were regressed against the number of active woodpecker groups in order to examine the relationship between the two. In a separate analysis, rates were standardized by the number of clusters occupied by resident woodpeckers. This number was corrected by deleting those clusters that had been captured. Captured clusters arise when a group residing in one cluster also occupies a second cluster formerly housing another group (Walters 1990).

TABLE 5.1. Percentage of cavity gains comprised of suitable, newly discovered cavities.

year	<i>FB</i>		<i>MACK</i>		<i>CNF</i>		<i>CL</i>	
	%	n	%	n	%	n	%	n
1981	35.5	31	100.0	6	--	--	--	--
1982	25.0	28	0.0	1	--	--	--	--
1983	11.5	26	42.9	7	--	--	--	--
1984	12.0	25	0.0	2	--	--	--	--
1985	21.4	28	0.0	4	--	--	--	--
1986	9.7	31	0.0	3	--	--	--	--
1987	0.0	22	0.0	2	--	--	55.6	9
1988	7.9	38	0.0	5	--	--	8.3	12
1989	8.8	34	25.0	4	84.2	19	0.0	15
1990	4.8	21	66.7	3	67.6	37	25.0	28
1991	20.0	20	50.0	2	35.0	20	5.0	20
1992	34.1	44	42.9	7	22.6	31	21.1	19
1993	28.1	32	12.5	8	21.4	28	23.1	13
1994	32.1	28	0.0	4	14.3	28	20.0	10
1995	6.3	16	0.0	2	20.0	45	13.8	29
1996	--	--	--	--	11.1	36	10.0	30
all years	18.4	424	28.3	60	32.0	244	16.2	185

Cavity Losses

Cavity loss is the result of an event or process that renders a cavity unsuitable or undesirable to red-cockaded woodpeckers. Because a generally agreed upon definition of what constitutes an unsuitable cavity does not exist in the literature, the definition used in these analyses was based on whether a cavity has been subjected to specific processes (see below). Regrettably, this confuses the analyses somewhat, as (1) a given process may have impacts of varying degrees on different cavities, such that a cavity is not always rendered unsuitable, and (2) when better cavities are unavailable, red-cockaded woodpeckers may still rely on cavities that were subjected to certain processes (Jackson and Parris 1995, Carter, pers. comm.).

There are several processes that result in cavity loss. Those taken into consideration in these analyses include (1) moderate or great enlargement of a cavity entrance or interior by another woodpecker species; (2) death of a tree housing a cavity; (3) physical separation of a cavity from the rest of the tree; (4) healing over of a cavity entrance following cavity abandonment; and (5) rotting out of a cavity bottom and hollowing out of a tree at a cavity bottom. While the last three represent the physical loss of cavities, enlargement of cavities and death of cavity trees represent functional losses. As discussed above, cavities subjected to enlargement and to tree death are still accessible to red-cockaded woodpeckers and are in fact used when better cavities are unavailable (Jackson and Parris 1995, Carter, pers. comm.). Use of cavities in dead trees for both nesting (Patterson and Robertson 1983) and roosting (Ligon 1970, Nesbitt et al. 1978) has been known to occur, even more than two years after the death of a tree (Hooper 1982). Despite this distinction between types of loss, and the implication it has for the differential use of cavities rendered unsuitable, all cavities that were lost were considered permanently unsuitable. The complexity of distinguishing between those cavities that are and are not used again following loss, as well as inconsistency in the collection of cavity data following tree death, prohibits such an analysis.

As discussed in Chapter 2, cavities that are abandoned by red-cockaded woodpeckers for long periods develop certain physical characteristics, based on which they are categorized as relict cavities. Even though the probability of their being used again is very low, cavities that became relicts without being subjected to the types of losses discussed above were not considered lost. Abandonment of cavities can, however, occur in response to losses not dealt with in these analyses. Cavities that are exposed to heavy fires may be abandoned if the cavity is destroyed or the entrance is enlarged by the fire such that it becomes unusable to the woodpeckers (Conner and Locke 1979). This results from the ignition of the cavity or cavity tree due to highly volatile turpenes contained in fresh resin surrounding the cavity (Conner and Locke 1979). Cavities may deteriorate in quality, or may be abandoned when sap flow is greatly reduced (McFarlane 1992, Walters, pers. comm.). Cavities may also be abandoned when the hardwood midstory surrounding a cavity tree grows to cavity level (Locke et al. 1983, Hovis and Labisky 1985, Conner and Rudolph 1991, Loeb et al. 1992), as occurs as a result of fire suppression. Encroaching hardwoods diminish the effectiveness of the resin barrier against predators by providing them with alternate routes to a cavity. These types of loss were not dealt with in the analyses due to unavailable or inconsistent data. However, losses of this kind are well-

documented as affecting the suitability of cavities to red-cockaded woodpeckers, and their absence from the analyses must be taken into account when interpreting the results.

Newly discovered cavities were considered candidates for loss only if they were suitable upon discovery. Newly excavated cavities that became unsuitable in the year of their completion, however, were considered to be both gained and lost in that year, even if they were already enlarged as non-completed cavities.

The same system as that employed for cavity gains was used in estimating the year of loss of cavities for which data were missing. In cases for which a coin toss was necessary, a single coin toss was used to estimate the year of death of a cavity tree, regardless of the number of cavities the death affected. Likewise, a single coin toss determined the year in which the section of trunk housing a particular cavity and any cavity above it broke from a cavity tree. However, separate coin tosses were employed to estimate the year of occurrence of different types of loss for those cavities subjected to more than one type of loss (e.g., tree death and cavity enlargement).

Cavity loss was not assumed to have occurred unless it was recorded, even when data were missing. Thus, although cavities that were not updated prior to the death of a cavity tree may have been lost by some other cause prior to the death, they were regarded as lost through tree death alone. Similarly, although it is unknown whether cavities that were lost-to-follow-up were subject to loss in the years they were not updated, the assumption was made that they were not. In some cases, however, these cavities were updated in the year following the end of a study and were found to have been lost. For these cavities, loss was assumed to have occurred during the study period and the year of their loss was estimated using the system described above.

Like gains, losses are reported as absolute numbers and as rates and compared between tree species. Rates of loss are presented both in standardized and unstandardized form. Standardized losses were expressed as the percentage of all suitable cavities that were lost each year. The number of suitable cavities was calculated for each year by adding the gains and subtracting the losses for that year from the number of suitable cavities in the previous year.

Losses were categorized by cause in an effort to identify the primary modes of loss operating in the different cavity populations, and their variation across years. In cases in which multiple causes were involved, loss of a cavity was designated as having occurred by the cause taking place in the earliest year. A hierarchy of losses was established in tabulating cavity losses resulting from multiple causes in the same year: cavities were preferentially reported as having been on a tree that died, then as having broken from a tree, and finally as having been enlarged. Additional analyses examined both the activity status of a cavity in the breeding season corresponding to the year of its loss and the status of the cluster from which the cavity was lost. The loss of cavities that were not actively being used at the time of loss or the loss of cavities in abandoned clusters may have less of an impact than the loss of cavities actively being used by the woodpeckers.

Common Cavities

Common cavities are generally regarded as the product of the excavation of two separate cavities that became physically connected (Walters, pers. comm.), resulting in a central chamber connected to the outside world by two or more entrance tunnels. In these analyses, common cavities were treated as if they had always existed as a single cavity, even if they existed as separate, completed cavities prior to becoming common. A newly completed cavity that became common with an already existing cavity was thus not tabulated as a gain. Loss of a common cavity could occur even when only one of the entrance tunnels was physically affected: for example, enlargement of one entrance tunnel, permitting access by larger species to the common cavity chamber or making the cavity harder to defend, would result in the common cavity being lost. When more than one entrance tunnel was enlarged and estimation of the year of loss required a coin toss, separate coin tosses were used for each of the entrance tunnels. The physical healing over of one entrance tunnel, however, did not result in loss of the common cavity: because the cavity could still be accessed from another entrance tunnel, it could still be used. Common cavities were somewhat problematic in regard to their activity status in the year of their loss, as individual cavity entrances were not always assigned the same status during updating. When activity status differed between cavities entrances, the status denoting the greatest level of activity was considered to be representative of the status of the common cavity.

Management Effects

Because the analyses sought to measure cavity turnover as a natural process, management measures designed to offset cavity loss were not incorporated into the calculations of gains and losses. Enlarged cavities that were fitted with restrictors were thus still considered enlarged. The effects of restrictors could not be totally controlled for, however, as cavities that were not enlarged were sometimes fitted with restrictors that may have acted to prevent subsequent enlargement. The impact of restrictors, artificially drilled cavities and cavity inserts is reported separately below. The effect of the use of these management tools on natural rates of gain was examined by comparing these rates between years in which they were used and years in which they were not used.

Effects on Estimation of Gains and Losses

Both the absolute numbers and the resulting rates of gains and loss were prone to error in estimation as a result of (1) newly discovered cavities, (2) cavities that were lost-to-follow-up, and (3) cavities for which no information regarding stage of excavation was recorded. As discussed above, newly discovered cavities that were unsuitable upon discovery were considered to be neither gained nor lost. As a result, both gains and losses were underestimated unless the cavities were part of a baseline population. Gains relating to newly discovered cavities may similarly have been overestimated in particular years and underestimated in other years if the year in which a cavity was completed did not coincide with the year in which it was discovered. Although the absolute numbers of gains and losses would be affected in both of these cases, the resulting measure of turnover would not be. This measure would be affected, however, in cases in which a suitable, newly discovered cavity that was considered a gain was completed in or prior

to the first year of a study. If this cavity was not subsequently lost, the resulting gains would have been overestimated relative to the losses.

As discussed earlier in the chapter, completed cavities that were lost-to-follow-up were assumed not to have been lost. This assumption may have led to an underestimation in the calculation of losses relative to gains, thus affecting the accuracy of the turnover rate. Cavities for which data regarding stage of excavation were unavailable were not included in the calculation of gains or losses. The exclusion of these cavities may have affected both gains and losses, but turnover would have been affected only if the cavities were not eventually lost or if they were lost-to-follow-up.

The percentage of cavities in each of the three categories is reported in order to evaluate their potential to affect the accuracy of the estimate of cavity turnover.

Results

Fort Bragg and Camp Mackall

Cavity Gains

The 1980 baseline population of suitable cavities consisted of 392 cavities on FB and 49 on MACK. Of these cavities, 320 were excavated in longleaf pine, 29 in loblolly and 43 in pond pine on FB. On MACK, 36 cavities were excavated in longleaf pine and 13 in loblolly. Added to the baseline population in subsequent years from new clusters on FB were 77 suitable cavities in longleaf, 13 in loblolly, 23 in pond pine and 1 in an undetermined tree species. Only ten cavities, all of them excavated in pond pine, were added to the baseline population for new clusters on MACK in subsequent years.

Annual gains in the number of cavities excavated in longleaf pine were more than ten times as great as those in either loblolly or pond pine on FB (Table 5.2) and twice as great on MACK (Table 5.3). Unfortunately these gains could not be correlated with the availability of each pine species, as availability data were not collected. Whether excavation by this population of woodpeckers was directed by preference for a tree species or by tree species abundance and distribution thus was not determined.

Cavity gains were broken down by year. The year of cavity completion was estimated according to the method outlined earlier for 6.6 % (n = 424) and 8.3 % (n = 60) of all cavities gained on FB and on MACK, respectively. Gains of completed cavities followed different patterns among the three pine species over the course of the study period on both FB (Figure 5.1) and MACK (Figure 5.2). The number of gains of cavities in longleaf pine was highly variable among years at both locations. The numbers of gains of cavities in loblolly and pond pine were lower and less variable (Figures 5.1 and 5.2). Variability between years in gains did not appear to be related to variability in the numbers of newly discovered cavities (Table 5.1).

TABLE 5.2. Turnover in completed cavities on FB between 1980 and 1995 by tree species. Turnover is expressed as both the difference between the absolute number of gains and losses of cavities and between annual rates of gains and losses. Gains include newly excavated cavities and suitable cavities that were already complete when first discovered.

	Longleaf	Loblolly	Pond	Unknown	All species
Total gained	367	30	20	7	424
Total lost	390	51	72	2	515
Gains - losses	-23	-21	-52	5	-91
Rate of gain	24.5	2.0	1.4	0.4	28.3
Rate of loss	26.0	3.4	4.8	0.1	34.3
Rate gain - rate loss	-1.5	-1.4	-3.4	0.3	-6
% of cavities lost	51.9	71.8	82.8	33.3	56.3

TABLE 5.3. Turnover in completed cavities on MACK between 1980 and 1995 by tree species. Turnover is expressed as both the difference between the absolute number of gains and losses of cavities and between annual rates of gains and losses. Gains include newly excavated cavities and suitable cavities that were already complete when first discovered.

	Longleaf	Loblolly	Pond	Unknown	All species
Total gained	33	12	14	1	60
Total lost	33	15	15	1	64
Gains - losses	0	-3	-1	0	-4
Rate of gain	2.2	0.8	0.9	0.1	4.0
Rate of loss	2.2	1.0	1.0	0.1	4.3
Rate gain - rate loss	0.0	-0.2	-0.1	0	-0.3
% of cavities lost	48.5	60.0	62.5	100.0	54.2

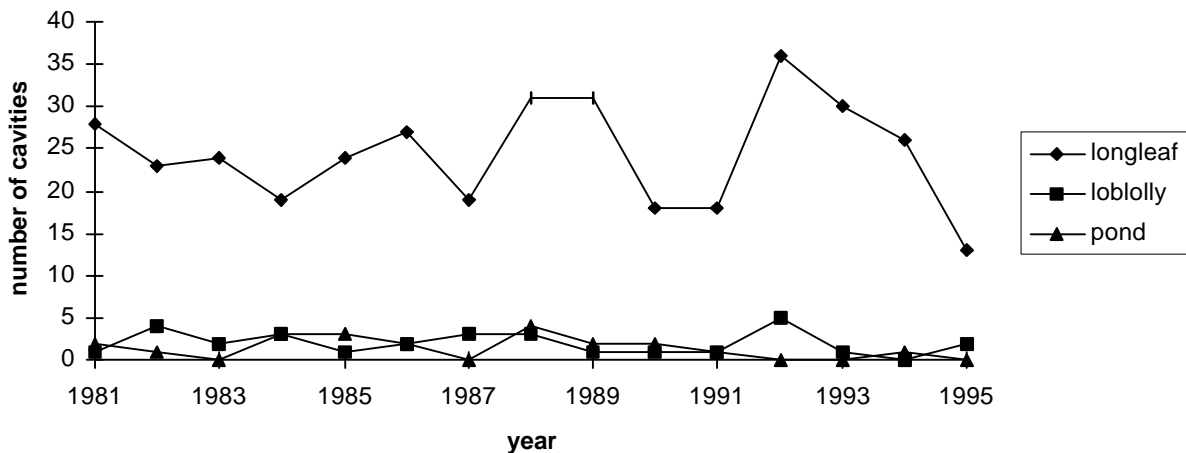


FIGURE 5.1. Yearly gains of completed cavities on FB in three tree species.

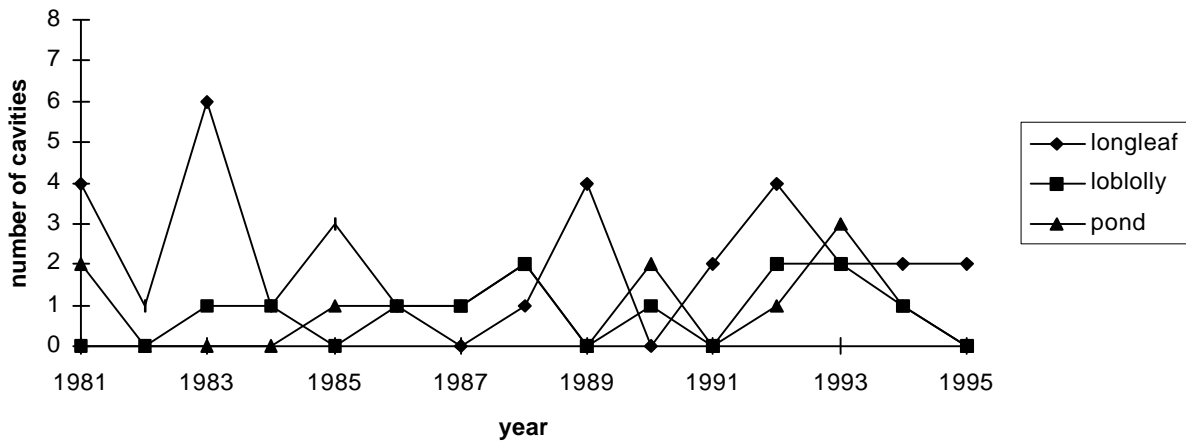


FIGURE 5.2. Yearly gains of completed cavities on MACK in three tree species.

The number of woodpecker groups in each study area was variable among years, fluctuating between 77 and 97 on FB (including solitary males, but excluding groups in artificial clusters) and nine and 13 on MACK. To separate the effect of the number of groups excavating from that of excavation activity, the relationship between cavity gains and the number of woodpecker groups was examined using linear regression. Gains were adjusted for FB by subtracting cavities gained on 19 clusters in the years in which those clusters were not checked for the presence of resident woodpeckers (1981-1984, 1995). Likewise, groups affiliated with clusters that were not checked and with new clusters checked after the first year of a study for the first time were not included. The curves representing number of groups and rates of gain followed dissimilar trajectories across the years (Figure 5.3), and there was no evidence of a linear relationship between the two variables ($R = 0.183$, $F = 0.033$, $p = 0.514$). Results were similar for Camp Mackall ($R = 0.090$, $F = 0.106$, $p = 0.750$), where the number of woodpecker groups was less variable across years (Figure 5.4). It is possible that the variability between years in the discovery of already completed, suitable cavities (Table 5.1) is confounding whatever relationship may exist between group number and cavity gains. Otherwise, variation in the number of gains appears to represent variation in excavation effort by the birds among years. This variability was quite evident when annual gains were standardized by the number of woodpecker groups present each year (Figures 5.5 and 5.6). There was some suggestion in these data of a reduced rate of gain in the 1990s.

Cavity Losses

Over one half of all suitable cavities were lost on both FB (56.3 %) and MACK (54.2 %) over the length of the study period. Annual losses of cavities in longleaf pine were three times as great as annual losses of cavities in all other species combined on FB (Table 5.2). This reflects the fact that the majority of completed cavities were excavated in longleaf pine on FB. Despite the fact that a larger pool of cavities had been excavated in longleaf pine on MACK, losses were

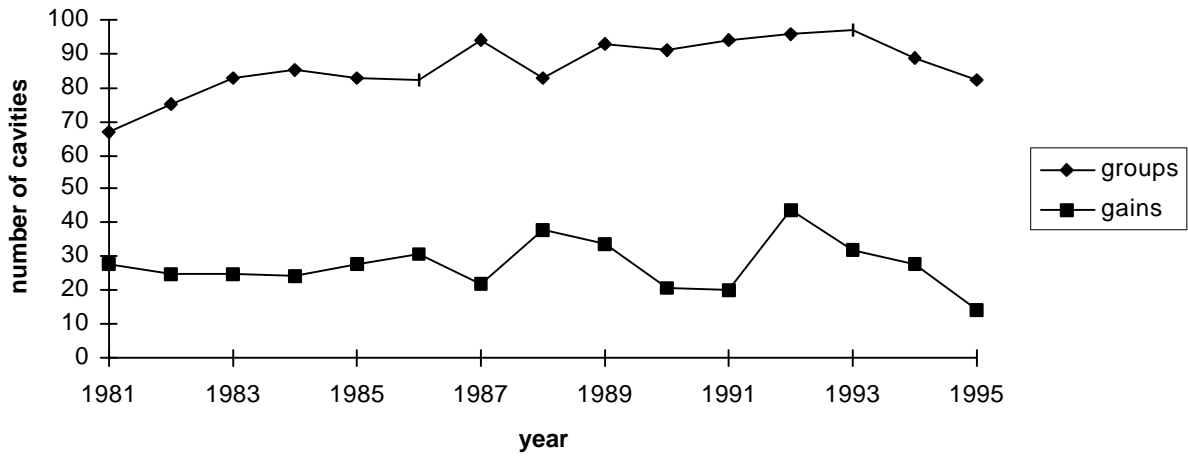


FIGURE 5.3. Numbers of red-cockaded woodpecker groups and gains of completed cavities on FB. Gains are combined across tree species.

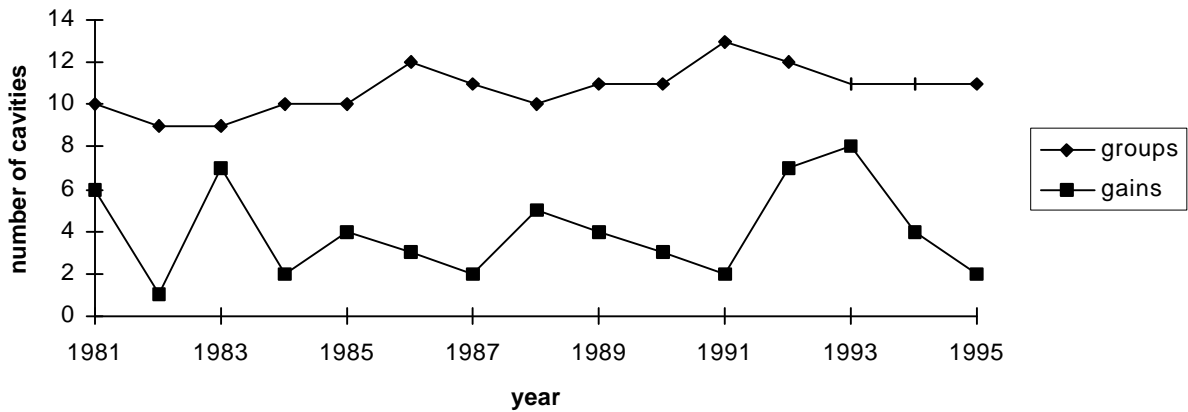


FIGURE 5.4. Numbers of red-cockaded woodpecker groups and gains of completed cavities on MACK. Gains are combined across tree species.

evenly divided between longleaf and the remaining species (Table 5.3). Losses exceeded gains for all species on FB, where there was an especially large deficit for pond pine (Table 5.2). On MACK, losses exceeded gains for pond pine and loblolly pine, but not for longleaf pine (Table 5.3). Losses were proportionally greater in loblolly and pond pine than in longleaf pine for both populations of cavities.

Cavity losses were broken down by year. The method outlined earlier was used to estimate the year of loss for 20.8 % (n = 515) and 29.7 % (n = 64) of all cavities lost on FB and on

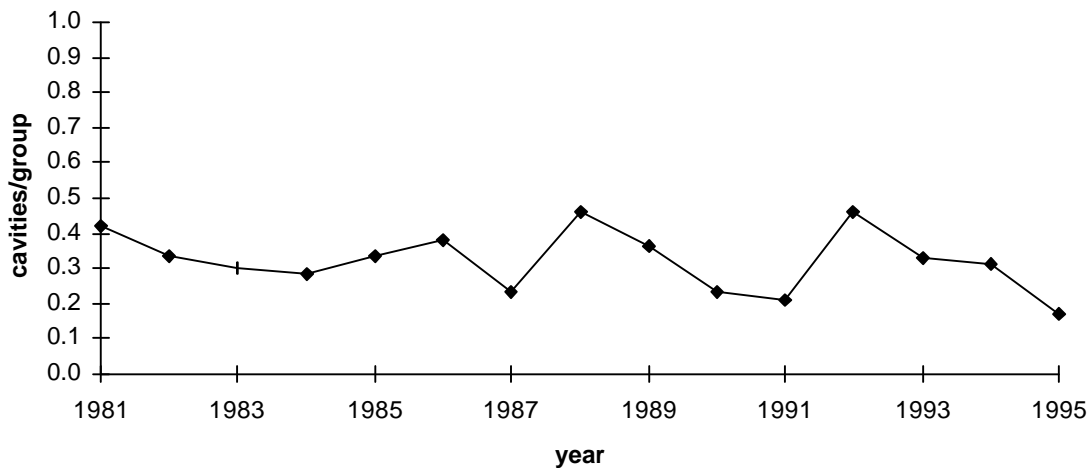


FIGURE 5.5. Cavity gains per group on FB.

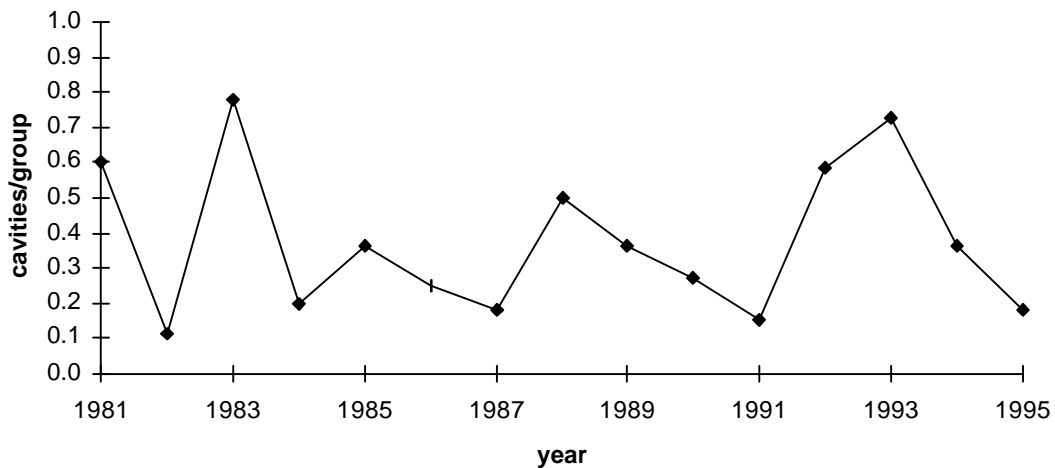


FIGURE 5.6. Cavity gains per group on MACK.

MACK, respectively. Yearly rates of cavity loss were fairly variable both between and within the different pine species on FB (Figure 5.7). The yearly variation in cavity loss on MACK was relatively low, but the number of cavities lost per year was small (range = 0 to 5 cavities). Some of the variability in losses among years was evidently due to variation in the standing population of cavities, as variability among years was less when losses were standardized by the current population of suitable cavities (Figures 5.8 and 5.9). Losses never exceeded 15 % of the yearly pool of suitable cavities for either cavity population. There was some indication in these data that the rate of loss increased in the 1990s (Figures 5.8 and 5.9).

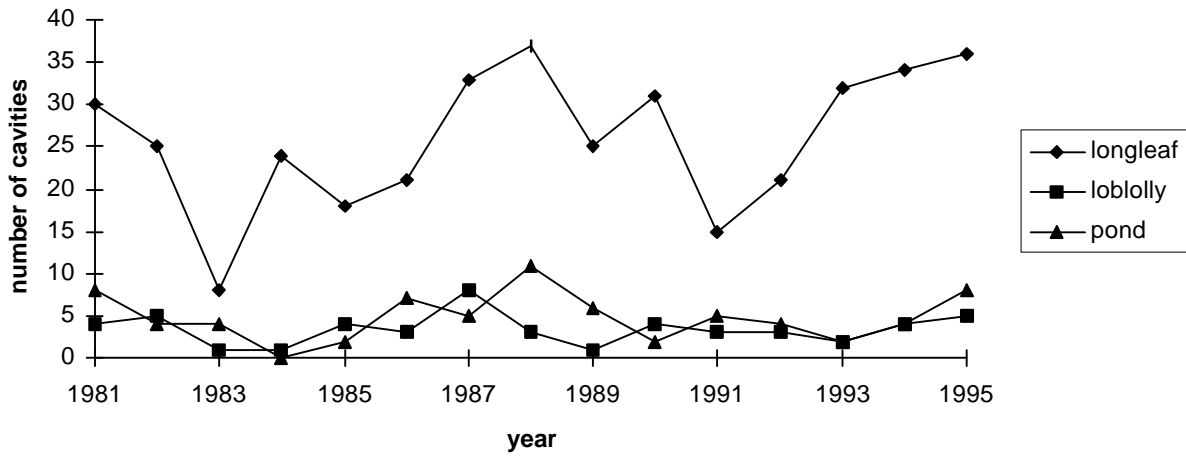


FIGURE 5.7. Yearly losses of completed cavities on FB in three tree species.

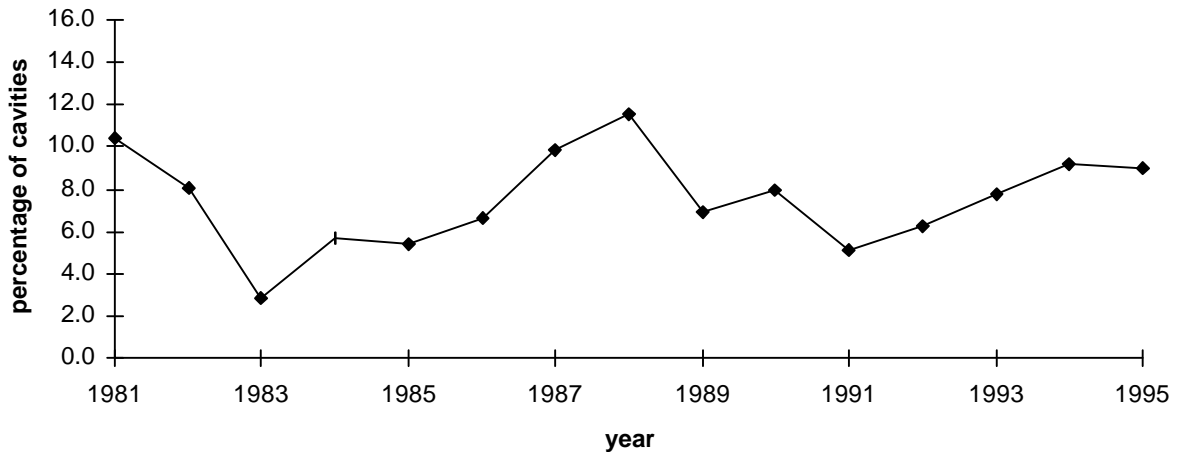


FIGURE 5.8. Percentage of suitable cavities lost on FB.

The activity status of each cavity was examined for the breeding season of the year in which it was lost. Of a total of 515 cavities lost on FB over the course of 15 years, 27.4 % were active, 8.2 % were possibly active, 26.6 % were inactive, 7.5 % were relicts, and 30.3 % were of unknown status when lost. On MACK, proportionally fewer cavities were being actively used when they were lost. Of 64 cavities that were lost, 18.5 % were active, 6.3 % were possibly active, 28.1 % were inactive, 15.6 % were relicts and 31.3 % were of unknown status. Because relict cavities have a low probability of being used again, losses of relicts likely are of little consequence to the woodpeckers. The percentage of relicts among lost cavities was relatively small, however, so that discounting losses of relicts would not significantly alter the rates reported in Tables 5.2 and 5.3.

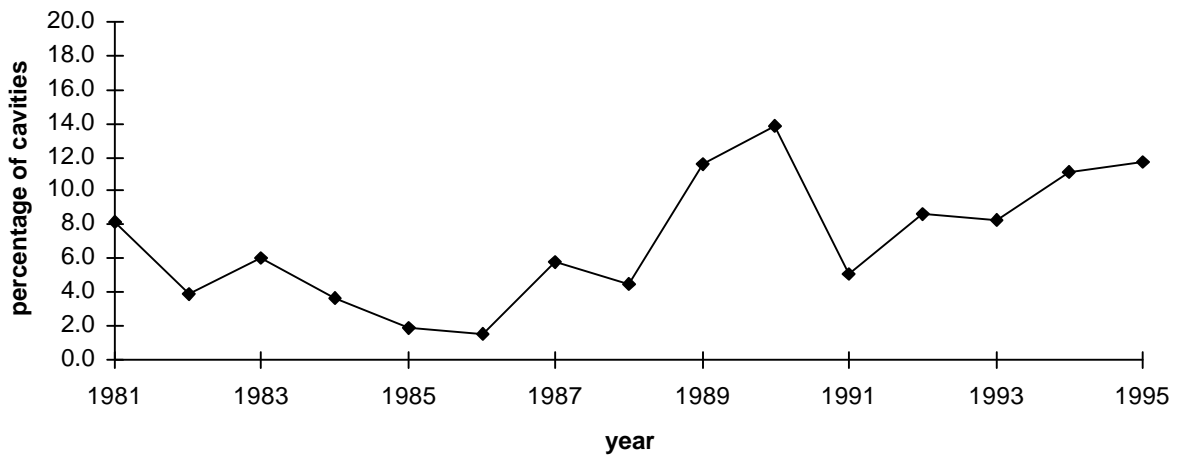


FIGURE 5.9. Percentage of suitable cavities lost on MACK.

A substantial percentage of the cavities that were lost were inactive. Their loss can not be dismissed in the same way as the loss of relics, however, given the potential for reactivation of inactive cavities (see Chapter 4). On FB, 11.5 % (n = 515) of cavities that were lost were in clusters that were abandoned in the year of the loss, of which 69.5 % were never reoccupied. Only seven of these 59 cavities were relics in the year of their loss. Of the cavities that were lost on MACK, 14.1 % (n = 64) were lost from abandoned clusters. All except one cluster remained abandoned. Of the cavities, four were relics in the year of their loss. Cavities lost on abandoned clusters, like losses of relics, are likely of little importance to the woodpeckers. In fact, the clusters may have been abandoned in response to low cavity quality. The percentages of cavities lost from abandoned clusters was, however, too low for their inclusion to alter the results significantly.

Patterns of loss were examined in relation to cause of loss. Cavity enlargement and cavity tree mortality were responsible for the majority of losses on both FB and MACK. This pattern was evident for all cavities, and even more so for active cavities (Figures 5.10 and 5.11). Through 1988, cavity enlargement accounted for the vast majority of losses on FB, but since then tree death has accounted for an increasingly larger, and enlargement smaller, proportion (Figure 5.12). In the 1990s these two factors have accounted for similar proportions of losses. Sample sizes were too small, and variability too great, to detect any changes over time in causes of cavity loss on MACK (Figure 5.13).

Cavity Turnover

Over the course of 15 years, there was one complete turnover of cavities. That is, the number of cavities gained over this period on FB (424) and MACK (60) exceeded or nearly exceeded the original population of suitable cavities (469 on FB and 59 on MACK), as did the number of

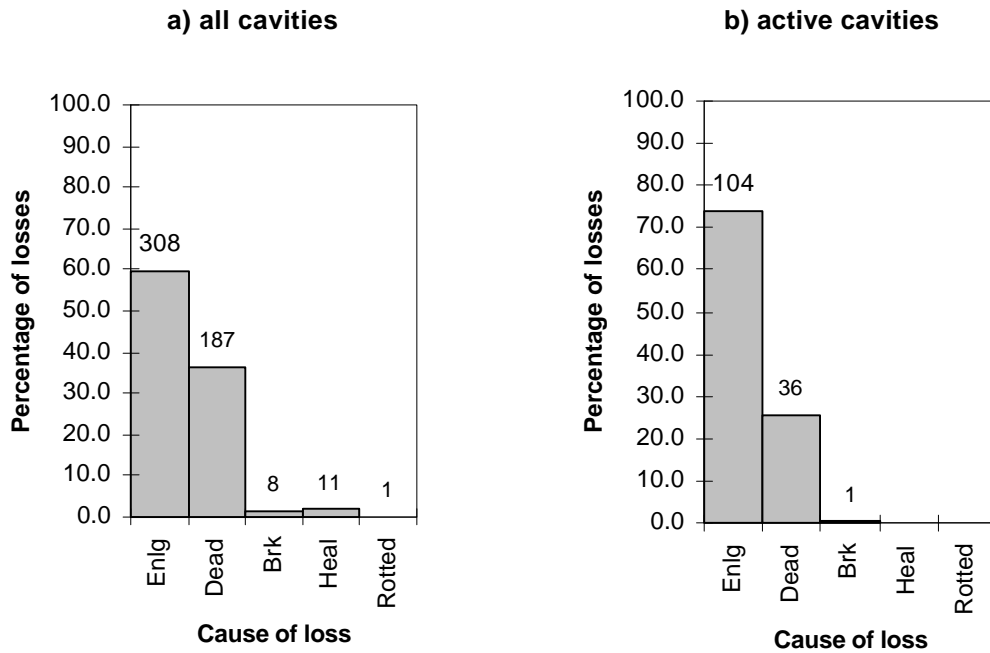


FIGURE 5.10. Causes of cavity loss on FB. Percentages reflect losses for all tree species. Percentages are shown for: a) all cavities, regardless of activity status in the breeding season of the year of their loss, and b) cavities that were active in the breeding season of the year of their loss. Causes depicted are cavity enlarged (Enlg), tree death (Dead), cavity broken off (Brk), cavity healed over (Heal) and cavity bottom rotted (Rotted).

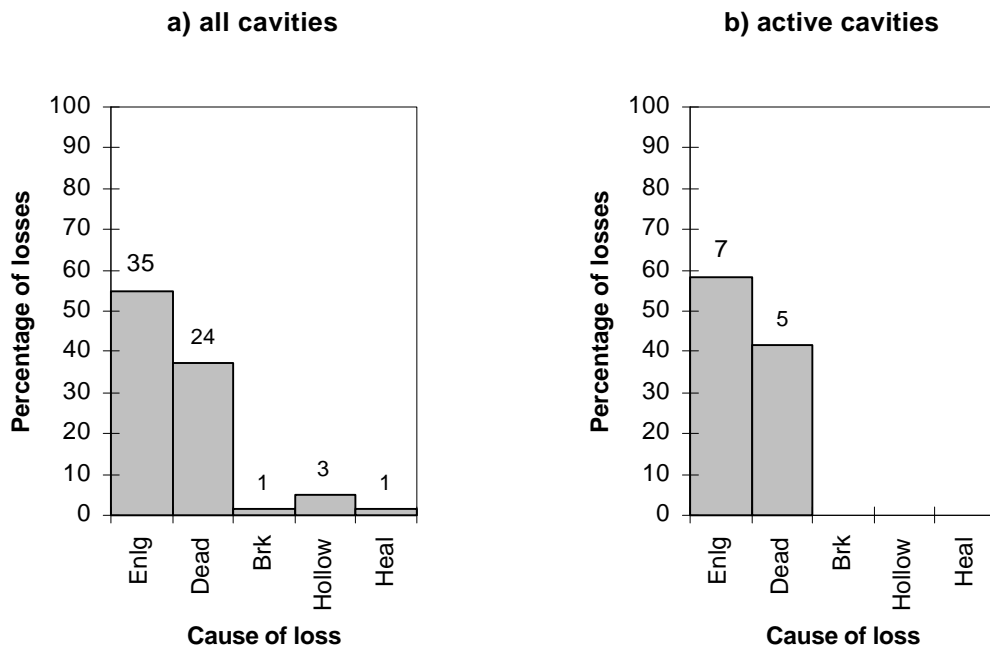


FIGURE 5.11. Causes of cavity loss on MACK. Percentages reflect losses for all tree species. Percentages are shown for: a) all cavities, regardless of activity status in the breeding season of the year of their loss, and b) cavities that were active in the breeding season of the year of their loss. Categories of loss are as in Figure 11, with the addition of tree hollow at cavity bottom (Hollow).

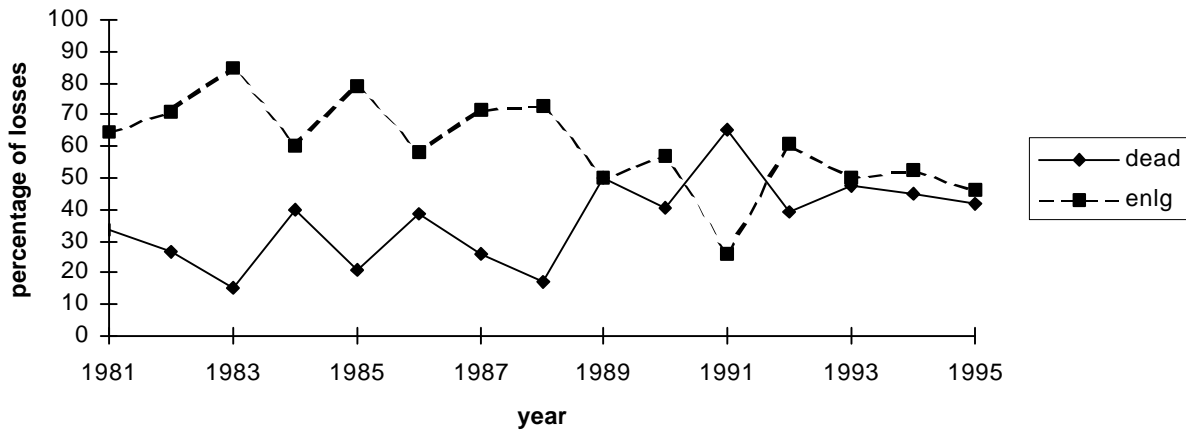


FIGURE 5.12. Percentage of lost cavities that were lost to enlargement and to tree death on FB. Percentages are combined across tree species.

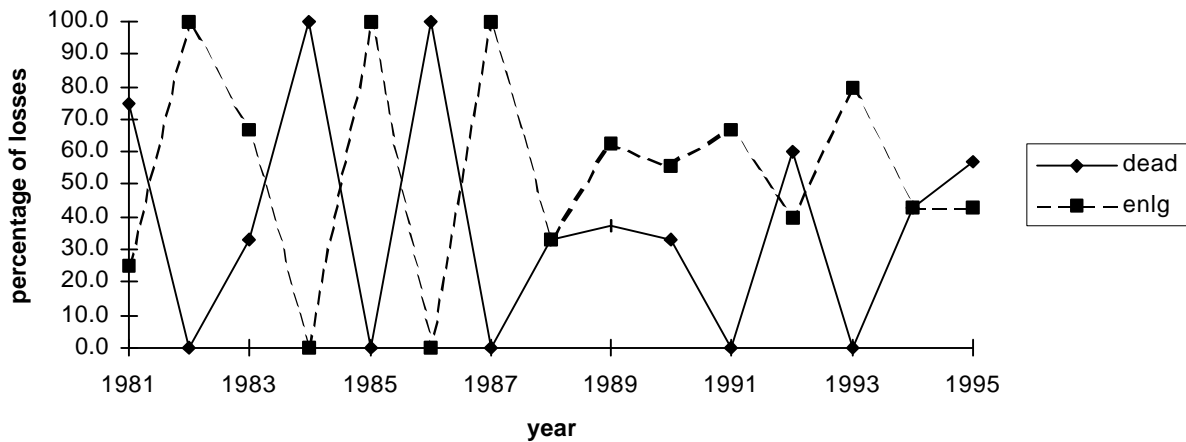


FIGURE 5.13. Percentage of lost cavities that were lost to enlargement and to tree death on MACK. Percentages are combined across tree species.

losses (515 for FB, 64 for MACK). The turnover time, based on these numbers, is roughly 15 years for both FB and MACK. Turnover time was calculated as the average of the time required to gain and the time required to lose as many cavities as those that made up the baseline cavity population, which here includes those baseline cavities discovered on new clusters (469 cavities on FB, 59 on MACK). On FB, gains exceeded losses in only four of fifteen years (1983, 1985, 1989, 1992; Figure 5.14), whereas on MACK there was no consistency in whether gains or losses were higher (Figure 5.15). Again, there appeared to be a tendency for the balance between gains and losses to be increasingly negative in the 1990s. Overall, woodpecker groups gained cavities at the rate of 0.32 (SD = 0.09) and 0.38 (SD = 0.21) per year on FB and MACK, respectively,

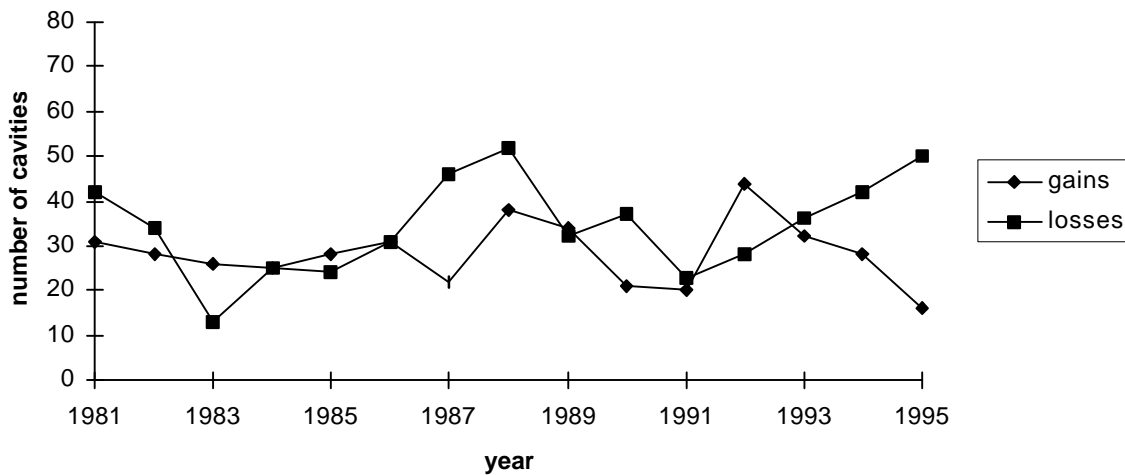


FIGURE 5.14. Rates of gain and of loss of completed cavities on FB. Gains and losses are combined across tree species.

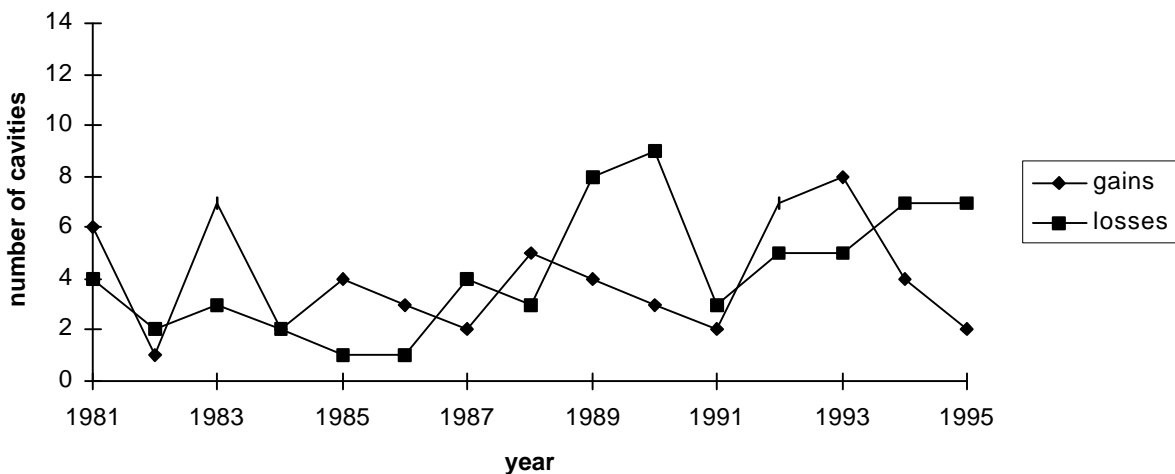


FIGURE 5.15. Rates of gain and of loss of completed cavities on MACK. Gains and losses are combined across tree species.

and lost them at the rate of 0.39 (FB SD = 0.19, MACK SD = 0.22) per year on both sites. Both gains and losses were adjusted for FB by subtracting cavities gained and lost on clusters that were not checked in certain years (see above). The similarity between rates of gain and loss resulted in a remarkable stability of the population of cavities suitable for roosting and nesting on MACK, where the 1995 population was smaller by only four cavities than the 1980 population. However, differences between rates on FB were large enough to result in a net reduction of 91 cavities. Excavation of new cavities by the woodpeckers thus appears to have compensated for the loss of

cavities on Camp Mackall, but has lagged behind the loss of cavities on Ft. Bragg. The deficit on both sites was smaller when cavities that were lost as relicts were discounted (see above), but the pattern remained.

As discussed previously, the accuracy of the estimate of turnover may have been affected by the inclusion and exclusion of certain cavities. Suitable, newly discovered cavities comprised a total of 18.4 % and 28.3 % of all cavities gained on FB and on MACK, respectively (Table 5.1). Of 78 such cavities on FB, 37 were subsequently lost. The difference between gains and losses may thus have been underestimated by as many as 41 cavities, potentially increasing the deficit of cavities by nearly fifty percent. Of the 17 suitable, newly discovered cavities on MACK, ten were subsequently lost. The difference between gains and losses was thus potentially underestimated by only seven cavities, which would translate into losses outnumbering gains by only 11 cavities. The exclusion of cavities for which data regarding the stage of excavation was unavailable may also have impacted the estimate of turnover. Sixty-nine such cavities exist on FB, but, because 64 of these were eventually lost, the estimate of the differences between gains and losses is potentially overestimated by a maximum of five cavities. Each of these five were lost-to-follow-up, so that their fate in the last year of the study was unknown. An additional cavity that was known to have been completed was also lost-to-follow-up. This cavity was a relict, however, and thus of little value to the woodpeckers. Overall, potential errors in the estimation of turnover may have had an effect on the magnitude of the differences between gains and losses, but not on whether these differences resulted in a surplus or in a deficit of cavities.

Management Effects on Cavity Turnover

The population of cavities available to red-cockaded woodpeckers has been supplemented since 1988 by the construction of artificial cavities on both FB and MACK. A total of 86 artificial cavities were either drilled or installed as inserts in trees in already existing clusters on FB. Fourteen of these cavities were not drilled to completion, but nine of these were excavated to completed cavities by red-cockaded woodpeckers. A total of eight artificial cavities were lost, but one of these, lost to enlargement, was regained by installing a restrictor. Of five artificial cavities on MACK, four were cavities drilled to completion and one was a drilled start completed by woodpeckers. Two of these cavities were subsequently lost. When artificial cavities are added into the calculations of gains and losses reported in Tables 5.2 and 5.3, the FB cavity population was smaller by 17 cavities than it was in 1980, and the MACK population was smaller by one. An additional 16 artificial cavities were used on FB to induce the formation of three new woodpecker groups. These groups were not included in any of the analyses. Nine of the cavities were drilled as starts, of which only three were completed by woodpeckers. Three completed cavities were lost. No cavities were excavated naturally by woodpeckers in these groups.

In addition, the loss of some naturally excavated cavities to enlargement was offset through the installation of cavity restrictors. Fifteen such restrictors were installed on enlarged cavities on FB, and two were installed on cavities that were not enlarged. Three of the enlarged cavities were subsequently lost to other causes, and one cavity was lost to enlargement following installation of the restrictor. One restrictor was removed or fell off subsequent to installation. No restrictors

were installed on MACK. When losses on FB were discounted by those cavities regained through the use of restrictors, the cavity deficit fell to six cavities.

The average rate of cavity gain per woodpecker group on FB was compared between those years during which artificial cavities and restrictors were not used (1981 - 1987) and those during which they were used (1988 - 1995). These rates were essentially identical (1981-1987 mean = 0.33 cavs/grp/yr, SD = 0.06, 1988-1995 mean = 0.32 cavs/grp/yr, SD = 0.11), suggesting that the rate at which the woodpeckers excavate was not influenced by the use of these management tools. Instead these tools have supplemented natural gains to positively impact cavity turnover. Indeed, during 1988-1995 the rate of gain of cavities through artificial means on FB was more than one third that of gains through woodpecker excavation.

Croatan National Forest

Cavity Gains

The 1988 CNF baseline cavity population consisted of 141 suitable cavities, 107 of which were excavated in longleaf pine, 32 in loblolly and two in pond pine. Twenty-three suitable cavities (15 in longleaf, four in loblolly and four in pond pine) were added to the baseline population of cavities from new clusters in subsequent years. The rate of gain of cavities in longleaf pine nearly doubled that of cavities in loblolly pine, and gains in pond pine were negligible (Table 5.4). As with FB and MACK, lack of tree species abundance data precluded determination of whether excavation of cavities in different species mirrored species availability.

Gains were broken down by year. The year of cavity completion was estimated according to the method outlined earlier for only 0.8 % (n = 244) of all cavities gained. Gains were highly variable between years (Figure 5.16): this variability could not be accounted for by variability in the numbers of newly discovered cavities (Table 5.1). Interestingly, gains followed similar patterns among the three species of pine, rising and falling fairly synchronously (Figure 5.16).

The number of clusters with resident woodpeckers was variable over the course of the study, fluctuating between 42 and 58 (including clusters with solitary males, excluding groups in

TABLE 5.4. Turnover in completed cavities on CNF between 1988 and 1996 by tree species. Turnover is expressed as both the difference between the absolute number of gains and losses of cavities and between annual rates of gains and losses. Gains include newly excavated cavities and suitable cavities that were already complete when first discovered.

	Longleaf	Loblolly	Pond	Other	Unknown	All species
Total gained	149	83	6	1	5	244
Total lost	151	82	7	0	1	241
Gains - losses	- 2	1	- 1	1	4	3
Rate of gain	18.6	10.4	0.8	0.1	0.6	30.5
Rate of loss	18.9	10.3	0.9	0.0	0.1	30.1
Rate gain - rate loss	- 0.3	0.1	- 0.1	0.1	0.3	0.4
% of cavities lost	60.2	73.9	58.3	0.0	33.3	63.8

artificial clusters). Variability in rates of gain did not appear to be related to these fluctuations (Figure 5.17). Standardization of gains by the number of woodpecker groups in fact did not decrease variability (Figure 5.18), and there was no evidence of a linear relationship between the two variables ($R = 0.457$, $F = 1.582$, $p = 0.255$).

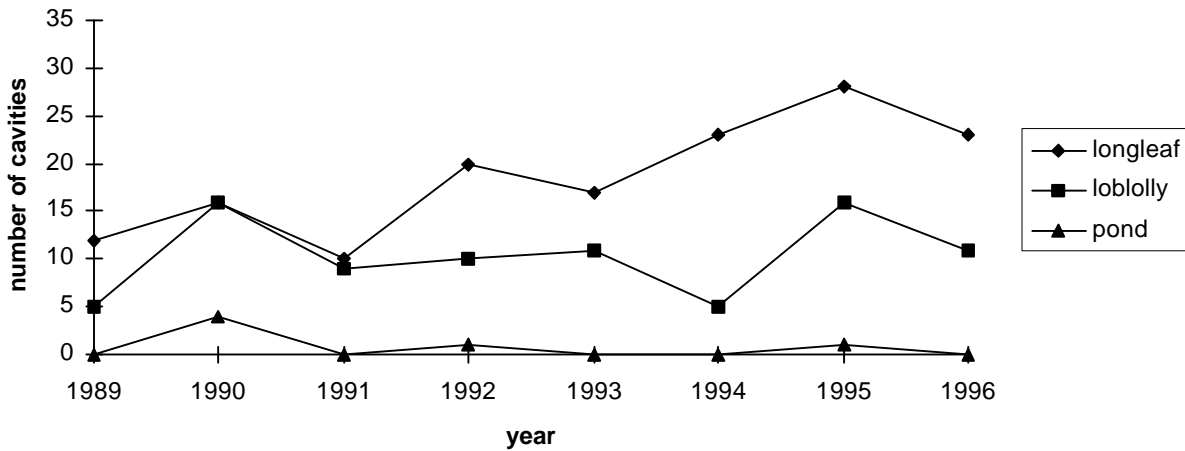


FIGURE 5.16. Yearly gains of completed cavities on CNF in three species of tree.

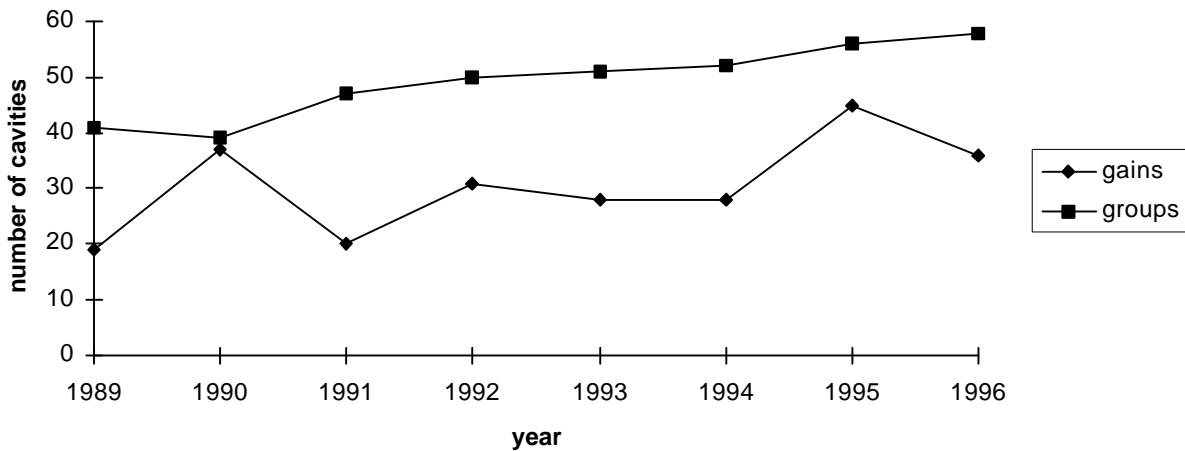


FIGURE 5.17. Numbers of red-cockaded woodpecker groups and gains of completed cavities on CNF. Gains are combined across tree species.

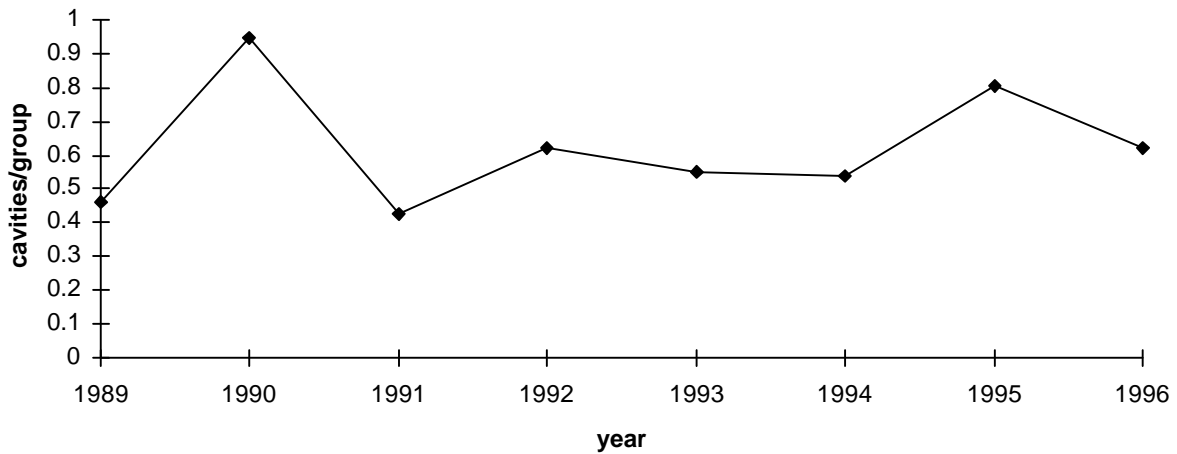


FIGURE 5.18. Cavity gains per group on CNF.

Cavity Losses

Rates of loss on CNF were remarkably similar to rates of gain for each pine species, so that the population in the last year of the study was greater by only three cavities than it was in 1988 (Table 5.4). Losses in longleaf nearly doubled those in loblolly, while losses in pond pine were few. As was the case in the Sandhills, losses of cavities excavated in loblolly pine (75 %) were proportionally greater than losses of cavities in longleaf (60 %), despite the fact that more cavities were excavated in the latter. The percentages of cavities lost were similar between longleaf and pond pine (Table 5.4).

Cavity losses were broken down by year. The method outlined earlier was needed to estimate the year of loss for only 1.2 % ($n = 241$) of all losses. Like gains, losses on CNF followed remarkably similar patterns between species over the years (Figure 5.19). The number of losses appeared to be unaffected by the number of suitable cavities, as losses standardized by numbers of suitable cavities were as variable among years as unstandardized losses (Figure 5.20). There was no obvious change in loss rate over time (Figure 5.20).

Of the 241 cavities that were lost, 49.0 % were active, 24.5 % were inactive, 9.1 % were possibly active and 14.9 % were of unknown activity status in the breeding season of the year of their loss. Only 2.5 % of cavities were relicts when lost. Along with an additional nine cavities, four of these relicts belonged to clusters that were abandoned in the year of their loss. However, only 37.5 % of these clusters remained abandoned for the remainder of the study. Given their numbers, the effect of relict cavities and of cavities in abandoned clusters on estimated turnover is negligible.

Cavity losses were broken down by cause of loss. Over 80 % of losses were the result of cavity enlargement, while the remainder were mostly due to tree death (Figure 5.21).

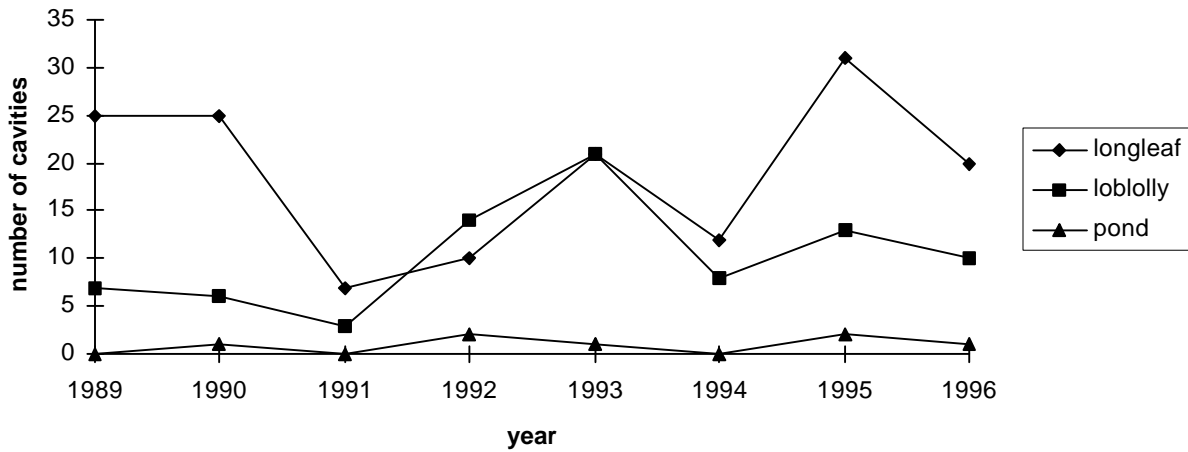


FIGURE 5.19. Yearly losses of completed cavities on CNF in three species of tree.

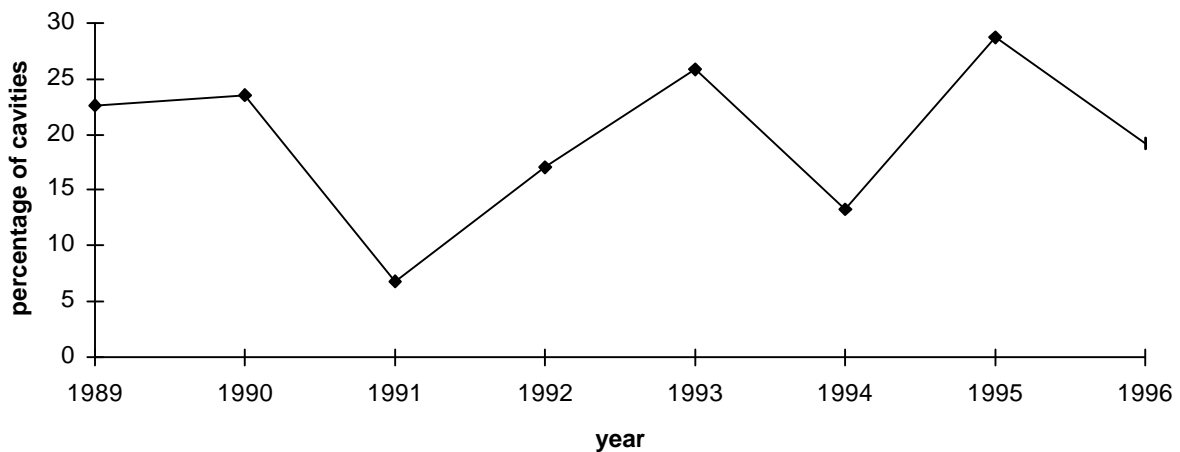


FIGURE 5.20. Percentage of suitable cavities lost on CNF.

Interestingly, the percentage of cavities lost to enlargement was even greater when only cavities that were active in the year of their loss were considered (Figure 5.21b). That losses by enlargement greatly outnumbered losses by tree death in nearly all years of the study confirms the greater significance of the former as an agent of loss (Figure 5.22). Other than an unusual proportion of losses due to tree death in 1992, causes of death were constant over time (Figure 5.22).

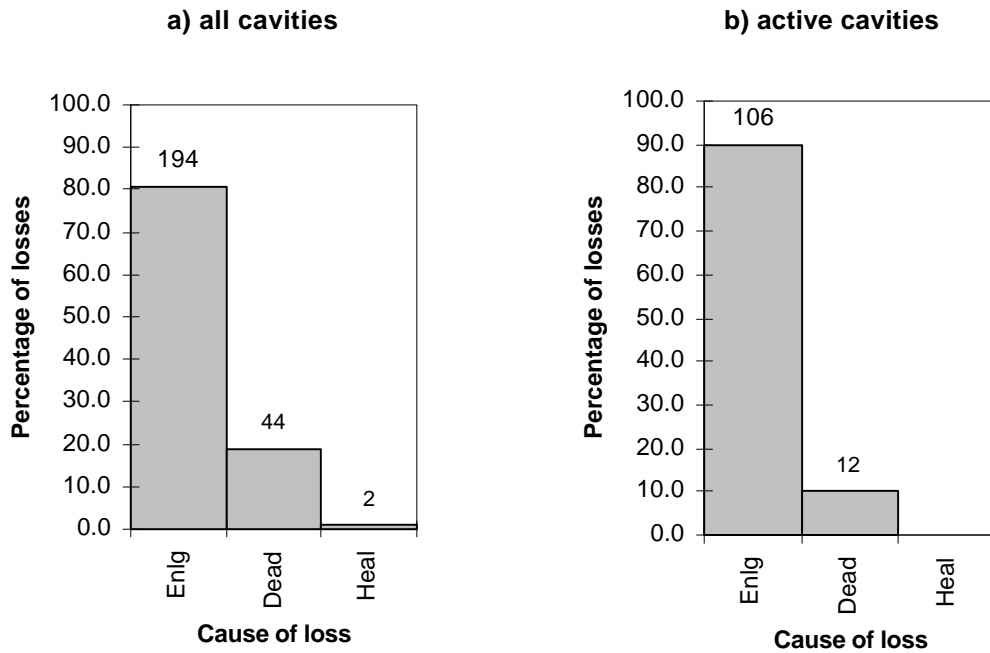


FIGURE 5.21. Causes of cavity loss on CNF. Percentages reflect losses for all tree species. Percentages are shown for: a) all cavities, regardless of activity status in the breeding season of the year of their loss, and b) cavities that were active in the breeding season of the year of their loss. Causes depicted are cavity enlarged (Enlg), tree death (Dead) and cavity healed over (Heal).

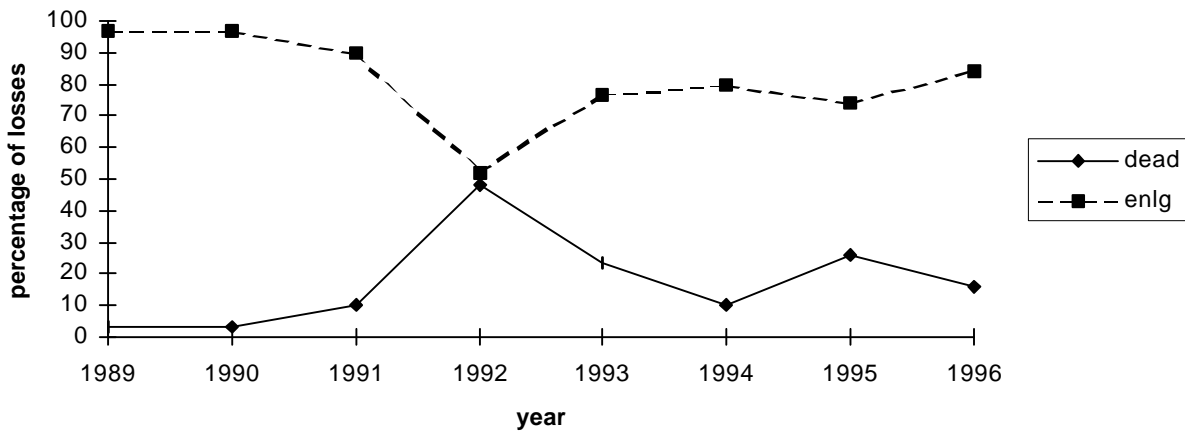


FIGURE 5.22. Percentage of lost cavities that were lost to enlargement and to tree death on CNF. Percentages are combined across tree species.

Cavity Turnover

The complete turnover of the population of cavities on CNF occurred over a surprisingly short period, estimated at approximately 5.4 years. This suggests that another complete turnover will have occurred by 1998. Although gains and losses alternately rose and fell throughout the study period, differences between them were never greater than 15 cavities in any given year, and were often less than ten (Figure 5.23). Both gains and losses underwent decreases in the last year of the study. Gains on CNF were estimated to have averaged 0.62 cavities per group per year ($SD = 0.18$) and losses 0.62 cavities per group per year ($SD = 0.24$) over the course of the study. As a result of the nearly identical rates, the population of cavities on CNF was remarkably stable, having increased over its original numbers by only three cavities over the eight year period.

The potential exists for miscalculation of the final balance of cavities between the first and last year of the study. Nearly one third of the 244 cavities gained on CNF consisted of suitable newly discovered cavities (Table 5.1). Of these 78 cavities, 43 were subsequently lost, and two were lost-to-follow-up. Cavity gains may thus have been overestimated by as many as 35 cavities, so that the difference between gains and losses may actually be negative. Information regarding stage of excavation was never recorded for cavities on 18 trees, which thus were not included in the calculations. Fourteen of these trees eventually died. It is unknown how many completed cavities were excavated in the remaining four trees, if any. An additional 11 cavities recorded as non-completed cavities were not followed consistently over the years: five of these were on trees that eventually died, but six were lost-to-follow-up. The potential existence of these unknown cavities suggests that gains may have been underestimated by ten cavities or more, although it is unknown whether any of these cavities were ever lost.

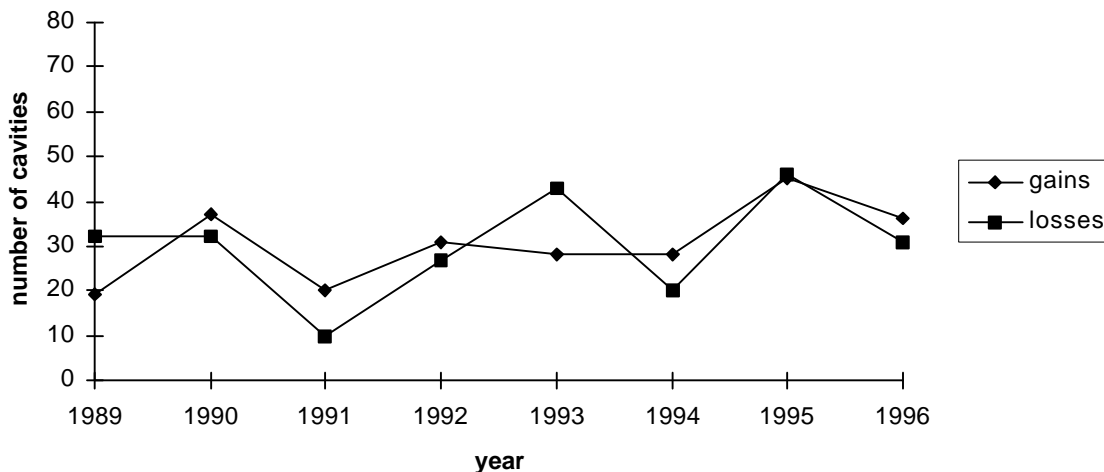


FIGURE 5.23. Rates of gain and of loss of completed cavities on CNF. Gains and losses are combined across tree species.

Management Effects on Cavity Turnover

A total of 105 artificial cavities were drilled in already existing clusters on CNF beginning in November of 1990. Sixty-four of these cavities were only drilled to the advanced start stage. Of these, 19 were completed by red-cockaded woodpeckers, resulting in a total gain of 60 completed cavities. Fourteen of these cavities were lost: 13 were enlarged and one was on a tree that died. Of the enlarged cavities, eight were regained through the application of cavity restrictors and not subsequently lost to other causes. Two additional cavities were restricted without having been enlarged.

Gains accounted for by artificial cavities increased the net gains reported in Table 5.4 by 54 cavities, so that the 1996 cavity population on CNF was greater by 57 cavities than the baseline population. An additional 45 artificial cavities were used to induce the formation of nine woodpecker groups on previously unoccupied habitat. All were drilled to the advanced start stage, and 19 were completed by red-cockaded woodpeckers. Two of these cavities were subsequently enlarged, but both were then restricted. No cavities were excavated naturally by woodpeckers in these groups.

The application of restrictors to enlarged cavities also offset total losses. Of 24 naturally excavated cavities receiving restrictors, four were on trees that subsequently died. The restrictor on another cavity was removed or fell off subsequent to installation. With the effect of both restrictors and artificial cavities factored into gains and losses, the net gain on CNF was of 76 cavities.

The average rate of cavity gain per woodpecker group on CNF was compared between those years during which artificial cavities and restrictors were not used (1989 - 1991) and those during which they were used (1992 - 1996). The rates were similar between the two sets of years (1989-1991 mean = 0.61 cavs/grp/yr, SD = 0.29, 1992-1996 mean = 0.63 cavs/grp/yr, SD = 0.11). Management practices thus do not seem to have negatively affected rates of natural cavity excavation. On the contrary, they have helped bring about increases in an already stable cavity population.

Camp LeJeune

Cavity Gains

The 1986 baseline population of suitable cavities on CL consisted of 118 cavities, 88 of which were excavated in longleaf pine, 22 in loblolly and seven in pond pine. Added to the baseline population in subsequent years from new clusters were only seven cavities, the majority of which were excavated in loblolly pine. Like cavity gains in the Sandhills and on CNF, the bulk of gains on CL were the result of excavation of cavities in longleaf pine, rates of which were nearly three times those of excavation in loblolly pine (Table 5.5). Pond pines did not appear to be a frequently used resource, with gains numbering less than ten cavities. Again, these data could not be related to tree species abundance.

TABLE 5.5. Turnover in completed cavities on CL between 1986 and 1996 by tree species. Turnover is expressed as both the difference between the absolute number of gains and losses of cavities and between annual rates of gains and losses. Gains include newly excavated cavities and suitable cavities that were already complete when first discovered.

	Longleaf	Loblolly	Pond	Unknown	All species
Total gained	125	43	7	3	178
Total lost	131	47	10	1	189
Gains - losses	- 6	- 4	- 3	2	- 11
Rate of gain	12.5	4.3	0.7	0.3	17.8
Rate of loss	13.1	4.7	1.0	0.1	18.9
Rate gain - rate loss	- 0.6	- 0.4	- 0.3	0.2	- 1.1
% of cavities lost	67.5	74.6	76.9	50.0	69.2

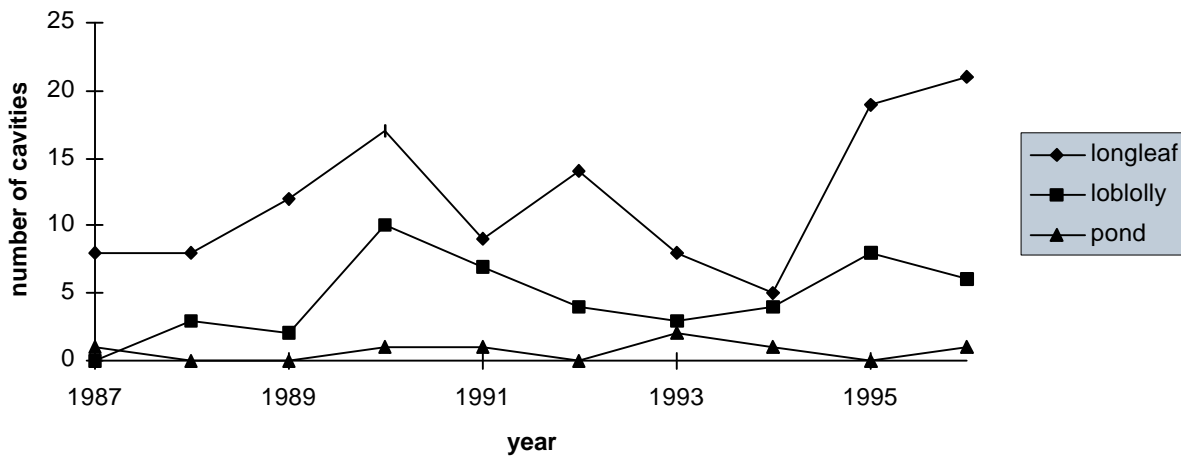


FIGURE 5.24. Yearly gains of completed cavities on CL in three species of tree.

When gains were assigned to different years, the year of cavity completion was estimated according to the method outlined earlier for only 3.4 % ($n = 178$) of all cavities gained. Gains were highly variable between years, and followed different patterns in different pine species (Figure 5.24). This variability did not appear to be associated with variability in the numbers of newly discovered cavities (Table 5.1), nor did it appear to be related to the number of active woodpecker groups in the population (Figure 5.25), which varied between 30 and 44 (including solitary males). The results of a regression of gains on number of groups were not indicative of a relationship between the two ($R = 0.485$, $F = 2.457$, $p = 0.156$), nor did standardization of gains by the number of groups have much effect on variability (Figure 5.26). Although rates of gain fluctuated between years, they appeared to be increasing in the last few years of the study.

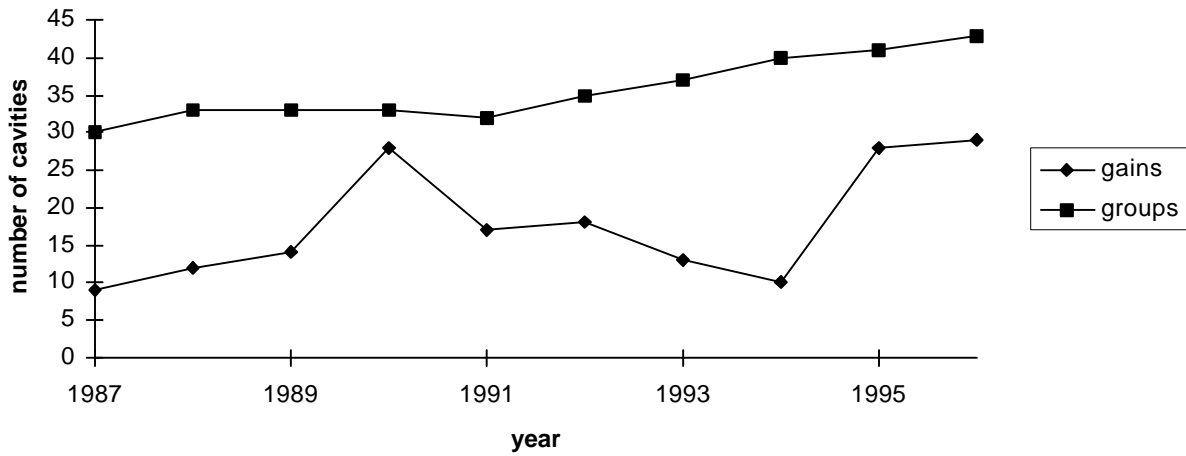


FIGURE 5.25. Numbers of red-cockaded woodpecker groups and gains of completed cavities on CL. Gains are combined across tree species.

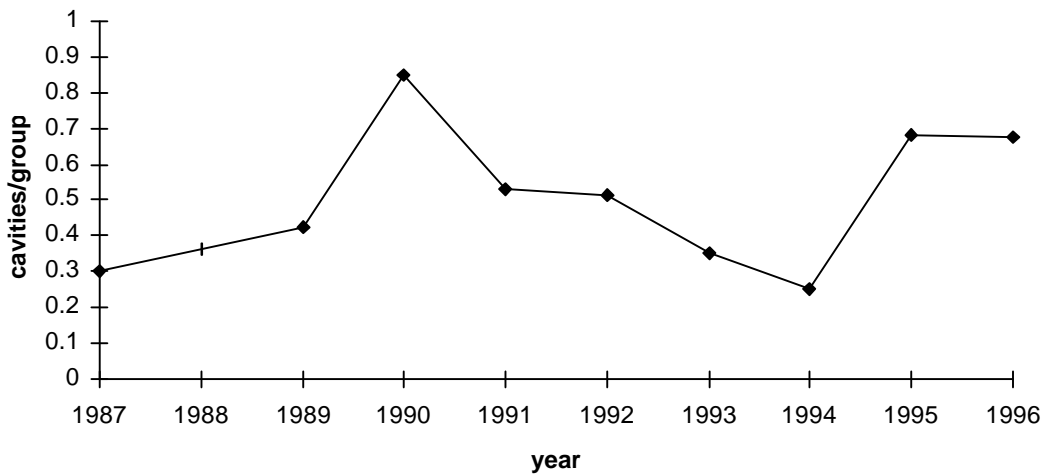


FIGURE 5.26. Cavity gains per group on CL.

Cavity Losses

Approximately 70 % of all suitable cavities on CL were lost over the course of the ten year study (Table 5.5). As on CNF, losses on CL were remarkably even with gains, resulting in only a slight deficit in the turnover of cavities between the cavity population in the first and last year of the study (Table 5.5). Again, the majority of losses occurred in longleaf pine and the fewest in pond pine. However, the percentages of losses for the various pine species were more similar

than they were in the Sandhills and on CNF, although the proportion lost was lowest in longleaf pine.

When losses were broken down by year, the method outlined earlier was employed in the estimation of the year of loss for 4.8 % of the cavities (n = 189). Losses were highly variable, both between years and between species (Figure 5.27). Although standardization of losses by the number of suitable cavities in the population greatly reduced variability, it did not eliminate it completely (Figure 5.28), suggesting that an interplay of different factors affected losses.

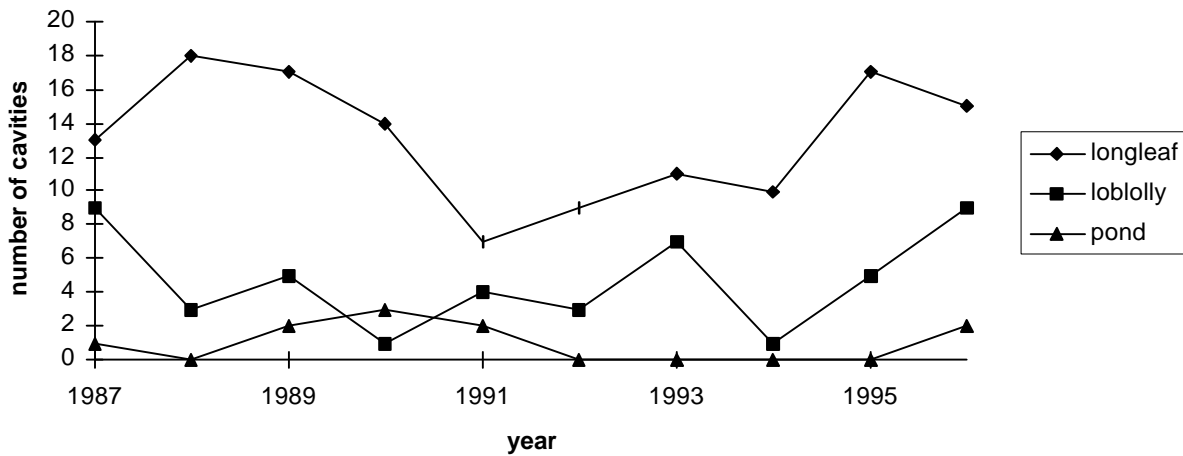


FIGURE 5.27. Yearly losses of completed cavities on CL in three species of tree.

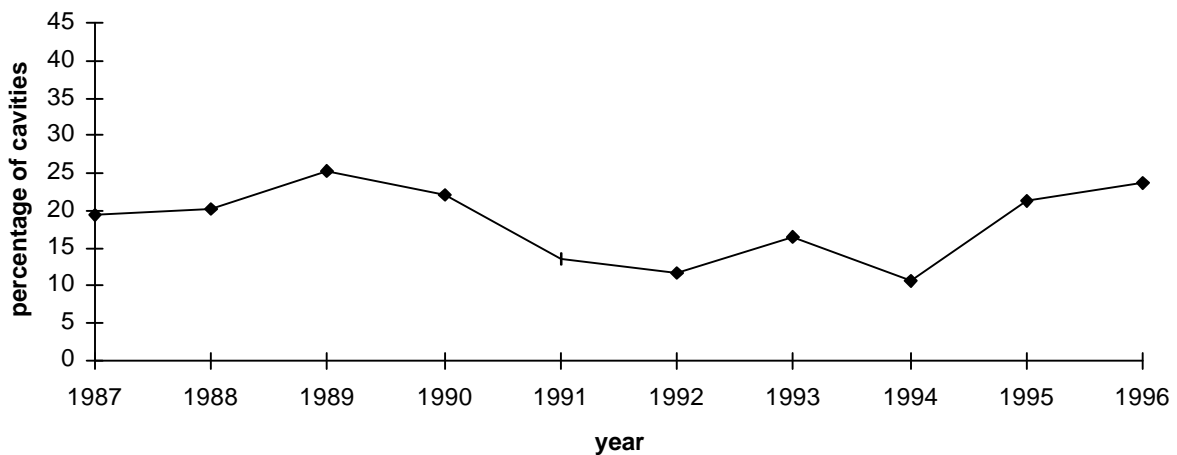


FIGURE 5.28. Percentage of suitable cavities lost on CL.

Losses were broken down by the activity status of cavities in the breeding season of the year of their loss. Of 189 cavities, 47.1 % were active, 25.4 % were inactive and 9.5 % were possibly active when lost. Relict cavities made up only 1.1 % of cavities that were lost, and cavities of unknown status accounted for the remaining 16.9 %. Only 1.6 % of the cavities lost on CL (n = 189) were in abandoned clusters. One of two such clusters was subsequently reoccupied. Two of the three cavities were lost as relicts, while the third was of unknown status but later became a relict. Eliminating relict cavities and cavities in abandoned clusters in computing losses would not have a significant effect on the estimation of cavity turnover for CL.

Approximately three quarters of all losses were the result of cavity enlargement by other woodpecker species, while the remaining cavities were lost due to tree death (Figure 5.29). Nearly 90 % of cavities that were active in the breeding season of the year of their loss were lost to enlargement (Figure 5.29b). Although both cavity enlargement and tree death were subject to variability over the years, losses by enlargement greatly outweighed losses by tree death except during 1991 and 1993 (Figure 5.30).

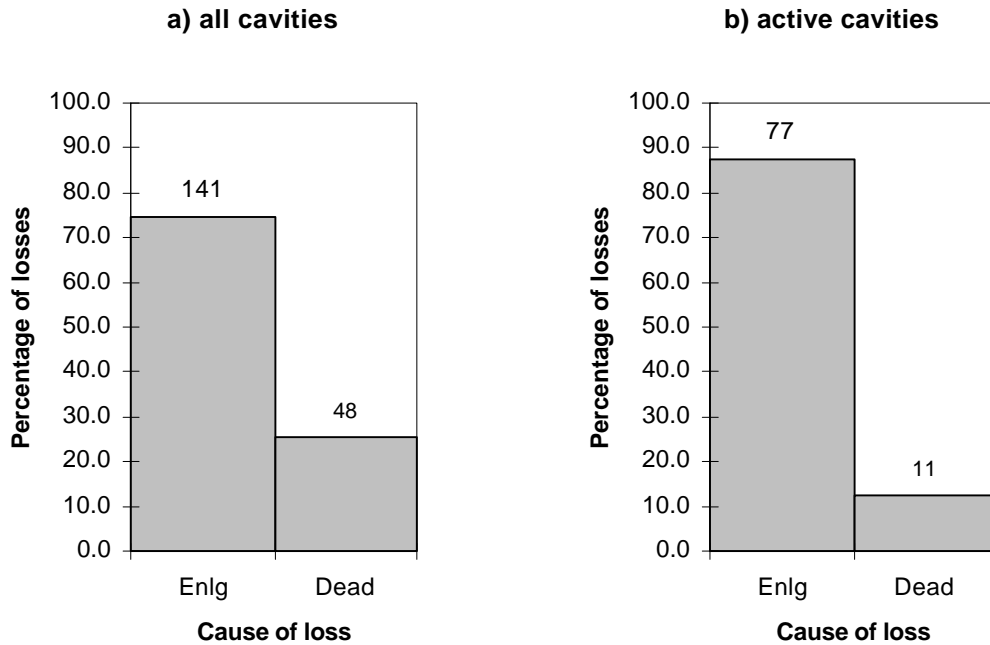


FIGURE 5.29. Causes of cavity loss on CL. Percentages reflect losses for all tree species. Percentages are shown for: a) all cavities, regardless of activity status in the breeding season of the year of their loss, and b) cavities that were active in the breeding season of the year of their loss. Causes depicted are cavity enlarged (Enlg) and tree death (Dead).

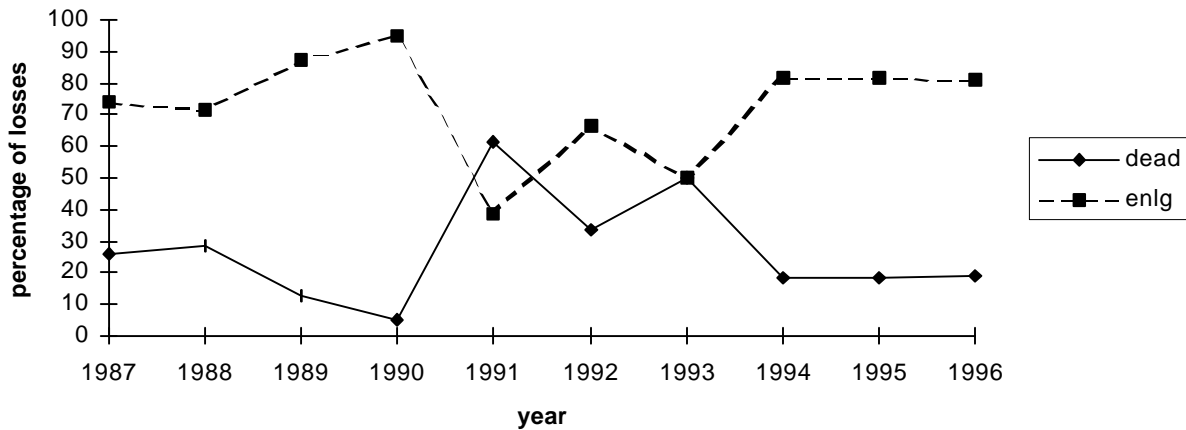


FIGURE 5.30. Percentage of lost cavities that were lost to enlargement and to tree death on CL. Percentages are combined across tree species.

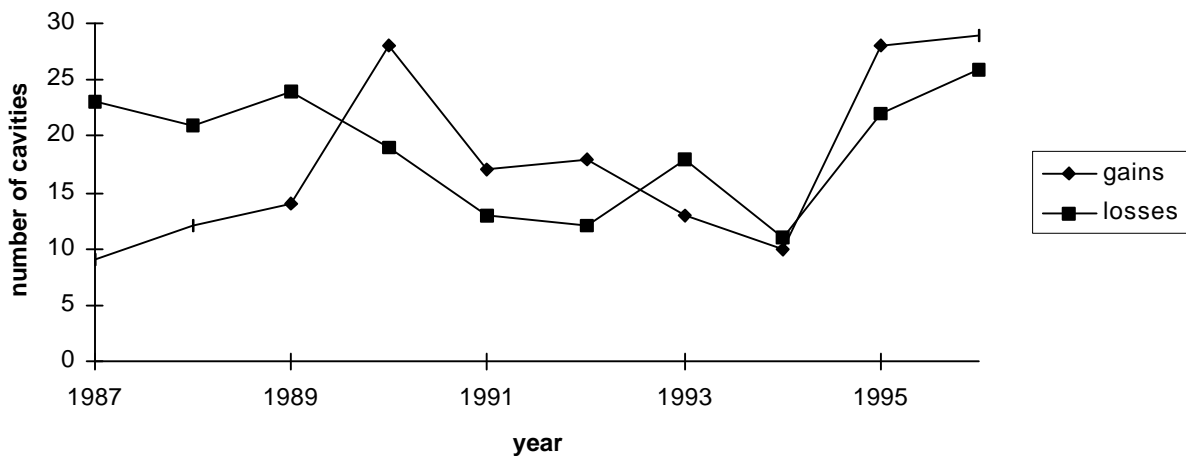


FIGURE 5.31. Rates of gain and of loss of completed cavities on CL. Gains and losses are combined across tree species.

Cavity Turnover

The complete turnover of the cavity population on CL was estimated as requiring 6.8 years, so that more than one complete turnover occurred over the course of the ten year study period. Rates of gains and losses were variable in relation toward one another throughout the study period. Both displayed a tendency toward increasing in the last two years of the study (Figure 5.31). Woodpecker groups on CL gained an average of 0.49 cavities per year (SD = 0.19) and lost an average of 0.54 (SD = 0.16). This translated into a net loss of only eleven cavities

between the first and last year of the study. Like CNF and MACK, the cavity population on CL showed great stability over time.

Approximately 16 % of the cavities gained on CL consisted of suitable newly discovered cavities (Table 5.1). One half of these 30 cavities were subsequently lost. An additional 21 cavities were not updated consistently after having been recorded as non-completed cavities, so that it is unknown whether any were ever excavated to completion. Twelve of these cavities were ultimately lost, and nine were lost-to-follow-up. Overall, net gains may thus have been overestimated by as many as 15 cavities and underestimated by a maximum of nine. The potential effect on the estimate of turnover of these possible biases thus is very low.

Management Effects on Cavity Turnover

A total of 82 artificial cavities, 63 of them drilled and 19 of them inserts, were installed on CL beginning in 1991. Twenty-nine of the former were drilled as advanced starts and ten were subsequently completed by the woodpeckers. Twelve completed cavities were enlarged: one was enlarged after a restrictor was removed or fell, and two others after they had already been restricted. No enlarged cavities were regained using restrictors, although a total of eight (including the three that became enlarged) were restricted preemptively. A total of 37 restrictors were used to offset losses of naturally excavated cavities (including two restrictors installed on separate entrances of a common cavity). Nine of these restrictors were installed on non-enlarged cavities (one on a relict non-completed cavity). Eight of the restricted cavities were in trees that subsequently died. Factoring the effect of both artificial cavities and restrictors into the calculation of turnover augmented net gains by 51 cavities and decreased losses by 18 cavities, resulting in a total net gain in the 1996 cavity population of 58 cavities over the 1988 population.

The average rates of cavity gain per woodpecker group on CL were similar between those years during which the management practices above were (1991-1996 mean = 0.50 cavs/grp/yr, SD = 0.17) and were not implemented (1987-1990 mean = 0.48 cavs/grp/yr, SD = 0.25). Rates of excavation therefore do not appear to have been negatively impacted by management practices. The use of these tools instead produced a surplus of cavities in an otherwise stable cavity population, accounting for nearly one half of natural gains between 1991 and 1996.

Discussion

Cavity Dynamics and Their Underlying Causes

Cavities are a valuable commodity to the red-cockaded woodpecker, given both the length of time required for their excavation (Chapter 3) and their potential for long periods of use following completion (Chapter 4). The number of woodpecker groups that a population can support is directly linked to the number of suitable territories, which is in turn linked to the presence of suitable cavities on these territories (Copeyon et al. 1991, Walters 1991, Walters et al. 1992b). In the past decade, the woodpecker cavity has been recognized as the key to the successful

management of this endangered species. The bulk of recent management effort and resources has in fact been directed to maintaining the suitability of existing cavities, to providing the woodpecker with new cavities, and to maintaining conditions on existing territories such that they are suitable for continued cavity use and for excavation of new cavities. It is therefore alarming that, in each of the cavity populations in my study, cavity gains are either lagging behind (FB) or barely keeping up with (MACK, CNF and CL) cavity losses. The estimates of duration of excavation and duration of use suggested that this might be the case (see Chapters 3 and 4), and the direct analysis of turnover confirms it. Furthermore, the calculations of cavity loss here do not include all factors that render cavities unsuitable. Most importantly, the calculations do not include encroachment of hardwood midstory on cavities or reductions in suitability caused by reduced sap flow. Also, field sampling was sufficient to detect only a portion of cavities that became unsuitable due to fungal rot. Actual losses of cavities from the woodpecker's perspective may thus very well be higher than the rates of loss calculated here. If this is the case, the deficit of cavities on FB is even higher, and whether the remaining cavity populations are really stable becomes questionable.

In the only previous analysis of cavity dynamics, Conner and Rudolph (1995a) measured turnover over a ten year period on the Angelina National Forest in Texas. Although they measured turnover of cavity trees, rather than of individual cavities, Conner and Rudolph concluded that, under the conditions experienced currently by the red-cockaded woodpeckers in the Angelina National Forest, the birds were not able to excavate cavities quickly enough to offset cavity losses. Conner and Rudolph sought to explain the disparity between gains and losses by the abundance and distribution of different-aged trees across the landscape. It is well known that the red-cockaded woodpecker depends on old-growth for cavity excavation (Jackson and Jackson 1986, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988, Rudolph and Conner 1991). Old-growth trees are found in increasingly smaller numbers, so that the woodpecker may be unable to excavate cavities at the rates they did historically because fewer trees are available for excavation. In addition, because younger trees, which are more widely available, are more susceptible to mortality, losses of cavities may be greater than they were historically if the woodpeckers are forced to excavate in these trees because of the dearth of older trees (Conner and Rudolph 1995a). Whether a larger pool of old-growth trees is available on CL and CNF than on FB is undetermined. It is clear from Chapter 3, however, that excavation in the two coastal populations requires less time than it does in the Sandhills. This may at least be partially responsible for the differences between cavity populations in balance between gains and losses.

Patterns of gains and losses appear to vary widely between the cavity populations in my study. This variation is not surprising, as habitat types, population dynamics and management regimes vary between the populations as well (Walters, pers. comm.). What each of the cavity populations has in common, however, is moderate to substantial variation in both cavity gains and losses over the course of each study period. Understanding the causes underlying this variation may be the key to more effective management of the cavity populations. The factors controlling cavity gains and losses and the variation associated with both are examined in the sections that follow.

Cavity Gains

The causes of the variability in cavity gains in each of the cavity populations are not easy to decipher, but certain elements can be readily eliminated. For example, it is clear that cavity gains are not correlated with woodpecker density in each of the study areas, despite the fact that density is subject to some variability. A more exact representation of the potential workforce available for excavation would be the number of individual woodpeckers residing on territories in the population, rather than the number of woodpecker groups. The number of woodpeckers in each group is in fact subject to potential variation between years (Lennartz et al. 1987). However, because it is unknown which and how many individuals in a group contribute to excavation, I am basing the estimate of potential excavators on the number of groups (the issue of excavation in relation to social status is explored in detail in Part II (Chapter 6)). In addition, the variability in gains may be a response to the availability of trees suitable for excavation from year to year. The availability of suitable trees is presumably controlled by two primary factors, tree mortality and tree age: the former makes trees unavailable, as the woodpeckers excavate cavities in living trees (Steirly 1957, Hooper 1982), and the latter makes them available, as the woodpeckers have a well-documented tendency to excavate cavities in old trees (Jackson and Jackson 1986, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Hooper 1988, Rudolph and Conner 1991). It is doubtful that the loss of trees from the pool of suitable trees, and the addition of trees to this pool as they age, would result in the erratic fluctuations in gains that are characteristic of each cavity population.

Given the elimination of the two factors with the greatest potential to explain variability in gains, the most likely explanation remaining is variation in excavation effort on the part of the woodpeckers. Although variation in effort is clearly consistent with the variation in excavation times addressed in Chapter 3, the underlying cause of variation in effort remains unknown. Cavity gains, which can be taken to represent effort, were demonstrated not to have been affected by management activities such as the use of restrictors and artificial cavities. The most promising possibility instead is that variation in effort is a response to cavity losses. However, a relationship between gains and losses is difficult to show, given that: (1) both are occurring simultaneously, (2) not all factors leading to the loss of cavities were included in my analyses (see above), and (3) there could be a time lag between losses and completion of replacement cavities (gains) due to the high time cost of excavation (see Chapter 3), even if increased effort in response to losses is immediate. In addition, loss of cavities from a cluster may provoke a response from the woodpeckers other than increased rates of excavation. For example, woodpeckers unable to keep up with losses in their cluster may abandon that cluster altogether, confounding the pattern of gains. The issue of the influence of cavity losses on excavation effort is addressed in greater detail in Part II (Chapter 6).

Cavity Losses

Like cavity gains, losses of cavities in all three tree species varied between years. Although some of the variability is explained by the standing population of suitable cavities, the magnitude of loss appears to be largely independent of the size of the standing population. Of the causes of loss examined, enlargement of cavities by other woodpecker species and cavity tree death account

for 90-100 % of all losses in all four study areas. Cavity enlargement is most likely affected by fluctuations in the populations of competing woodpecker species or in the availability of snags for cavity excavation by these other species. Explaining variation in cavity tree mortality requires a closer look at the causes of tree death. Of the cavity trees that died on FB, nearly one third were lost to fire-related causes (Table 5.6). On MACK, losses related to fire and to wind were proportional to one another, with mortality from lightning strikes accounting for the bulk of the remaining losses whose origin was identifiable (Table 5.6). On CNF, beetle (*Dendroctonus frontalis* and *Ips* spp) infestations and wind made up one third and one sixth of all losses, respectively, with fire accounting for only ten percent of losses. On CL, losses were fairly evenly divided among fire, beetle infestations, lightning strikes and wind-related causes. Variation in tree mortality in each cavity population can only be partially explained by variation due to these causes of loss, however, as losses due to unknown causes are fairly substantial in each study area, varying from approximately 30 to 60 %. Such losses are believed to be related to tree stress (Walters, pers. comm.), which in turn may be due to a number of causes, including fungal infestation and old age. Overall, variation in cavity mortality thus appears to be due to variation in climatic factors (wind, lightning), stress, beetle infestations, and fire. Of these, only the last two can be effectively managed. This issue is discussed further in the next section.

Cavity Population Management

Based on the information presented above, it is clear that certain factors responsible for the current status of each cavity population are beyond human control, while others can be directly managed. Cavity enlargement cannot be controlled directly. Instead, it is best dealt with through the preemptive installation of cavity restrictors or through their use following enlargement (Carter et al. 1989). The durability of cavity restrictors and their effectiveness in preventing access to enlarged cavities by larger species still requires confirmation, however: as seen on CL, enlargement of cavities can occur even after the cavities are restricted. Although tree death is not contributing to losses as much as is cavity enlargement, its importance should not be underestimated. Had they not been enlarged, cavities that were enlarged in many cases would have been lost through tree death shortly afterwards, so that potential loss of cavities by tree death is somewhat underestimated. In addition, whereas enlargement affects individual cavities, tree death can result in the simultaneous loss of multiple cavities on trees in which more than one cavity has been constructed. Most importantly, whereas cavity enlargement can be reversed through the use of restrictors, tree death is irreversible, and is contributing to decreases in the

TABLE 5.6. Percentages of trees dying by cause of death.

Cause of death	<i>FB</i> (n = 148)	<i>MACK</i> (n = 17)	<i>CNF</i> (n = 41)	<i>CL</i> (n = 42)
Fire	32.4	17.6	9.8	8.9
Wind	8.1	23.5	17.1	6.7
Lightning	4.1	11.8	7.3	8.9
Beetles	1.4	5.9	34.1	9.5
Flood	2.7	0.0	0.0	0.0
Other	2.7	0.0	2.4	2.2
Unknown	48.6	41.2	29.3	57.8

already small pool of old-growth trees on which the woodpecker depends for cavity excavation.

Although loss of cavities through tree death can be compensated through the use of artificial cavities, protecting old-growth trees, whether they currently contain a cavity or not, should become a management priority. As discussed above, preventing tree mortality in many cases is beyond the reach of current management techniques, but in other cases can be averted. An example of preventable cavity loss is loss through fire-related mortality, which is substantial on FB. Such losses may stem from: (1) accumulation in clusters of hardwoods that serve as fuel to create fires of intensities that the normally fire-resistant pines are unable to withstand; and (2) high-intensity fires during controlled burns (Conner and Locke 1979). Care should be taken to keep fire intensity low when burning woodpecker clusters (Conner and Locke 1979) containing old-growth, and combustible material should be raked away from the base of trees containing cavities (Conner and Locke 1979). Back fires should be employed to prevent accumulation of fuel in the years between prescribed burns (Conner and Locke 1979). In addition, mechanical removal of combustible hardwoods from cavity clusters containing old-growth should be employed when fire has failed to kill the encroaching hardwoods. Old-growth trees should be excluded from timber harvest operations and protected from other human activities that might threaten them.

Tree death resulting from beetle infestations in the coastal populations has not yet reached the epidemic proportions that it has elsewhere (Conner and Rudolph 1991, Coulson et al. 1995, Rudolph and Conner 1995). However, cavity losses due to this particular cause are fairly substantial, and may be controlled through proper management, mostly through preventive silvicultural practices designed to reduce the probability of beetle attack (Nebeker et al. 1995, Rudolph and Conner 1995).

The present status of each cavity population is a byproduct not only of cavity losses, but of gains as well. Although there is still much to be learned about the mechanisms responsible for the patterns of gains in each of the cavity populations, the utility of management tools such as artificial cavities in slowing or even reversing negative trends in gains has been amply demonstrated. It is clear that artificial cavities are used by red-cockaded woodpeckers, who will even complete excavation of partially drilled cavities (Copeyon 1990, Copeyon et al. 1991, Walters et al. 1992b, Walters et al. 1995a and b). In Chapter 4, it was shown that artificial cavities have potential as nests that rivals that of naturally excavated cavities, although more data are required in order to determine their potential as roost cavities. Artificial cavities can be essential to achieving stability in cavity populations, as was proven on FB. Construction of artificial cavities in recent years has resulted in a reduction of the negative balance, or in an increase in the positive balance for cavity turnover, at least for cavities lost to external causes. Because the number of woodpecker groups in a population depends heavily on the number of suitable cavity tree clusters available, artificial cavities are a powerful tool in the management of this species.

The installation of artificial cavities is more costly and labor intensive than is the installation of cavity restrictors. As discussed above, restrictors counteract losses to cavity enlargement, whereas artificial cavities may compensate for reduced rates of gain and for losses of cavities

through tree death. Given the trend in recent years toward decreasing gains and the increasing importance of tree death as a cause of cavity loss on FB, it is becoming increasingly necessary to employ the more expensive technique of artificial cavity construction in this study area. The situation on FB is in fact the worst possible: gains are currently decreasing and losses are simultaneously increasing. Given that the use of restrictors on FB has been limited to less than 20 units since 1988, increasing the installation of these devices can be used to counteract cavity losses rather cheaply, given the predominance of cavity enlargement in this study area. The pattern of gains and losses on MACK has been similar to that on FB in the past few years. However, gains have generally compensated for losses and the cavity population is relatively stable as a result. Given the small number of woodpecker groups on MACK, the use of artificial cavities may perhaps better serve for expansion of the bird population through induction of new group formation.

The outlook for both coastal cavity populations is also more favorable than it is for FB. On both CNF and CL, gains and losses alike showed tendencies toward increasing toward the end of each study. Cavity enlargement has and continues to be responsible for the majority of losses in both cavity populations. Here, the use of artificial cavities to offset cavity losses and to supplement cavity gains is not as imperative as it is on FB, given the relative stability of the cavity populations and the relatively low contributions to loss from tree death. Restrictors should be effective in counteracting the majority of cavity losses. The focus here, as on MACK, should be on expansion of the woodpecker population beyond the existing clusters: use of artificial cavities to induce new group formation, rather than to supplement already existing territories, should thus be prioritized. This has already been taking place on CNF since 1991, but has so far been limited to the reclamation of abandoned territories on CL (Walters, pers. comm.).

Knowing that territory occupancy is dependent on the presence of suitable cavities (Copeyon et al. 1991, Walters 1991, Walters et al. 1992b), the implication of my findings is that cavity availability needs to be continuously monitored on a territory by territory basis. The advantage of continuous monitoring is that cavity deficiencies on individual territories can then be compensated by installation of cavity restrictors and construction of artificial cavities. The need for artificial cavity construction especially will persist for many years, although its importance will vary between cavity populations. Even in the cavity populations that currently appear to be stable, however, cavity dynamics are associated with an environment in which cavity excavation and loss is restricted almost entirely to a small, declining pool of old-growth trees. This environment will persist for the next few decades, until second-growth trees are sufficiently old that they become suitable for cavity excavation. Excavation may become increasingly difficult as the number of old-growth trees not yet used becomes smaller and smaller, further reducing the bird's ability to be selective, and rates of loss will increase as the old-growth trees age. Cavity dynamics are thus likely to deteriorate, and the woodpeckers are likely to become increasingly dependent on artificial cavities.

Part II

Chapter 6: Social Dynamics of Cavity Excavation

Introduction

The explosion of literature on the red-cockaded woodpecker in the past 25 years has made it one of the more studied avian species of recent times. Largely prompted by the woodpecker's endangered status, much of the work has been management oriented, focusing on the role of the cavity as a critical resource to the bird. Studies of cavity excavation have tended to emphasize habitat-related variables, such as the factors influencing the bird's selection of pine species and of individual trees (Conner et al. 1976, Jackson 1977b, Conner and Locke 1982, Hooper 1988, Hooper et al. 1991, Rudolph and Conner 1991), and more recently have dealt with the physical dynamics of excavation (Conner and Rudolph 1995a, Chapter 3). As argued in Part I, the dynamics of the excavation process are implicated as the ecological basis for the selection for delayed dispersal of some male individuals. The evolution of delayed dispersal in turn set the stage for the development of the woodpecker's cooperative breeding system. Part II examines the social dynamics of excavation, rather than the physical process or its evolutionary significance.

Cavity excavation requires an average of 6.5-13 years, depending on the pine species and on the particular population (Chapter 3). That the process is so lengthy is in large part due to the difficulties inherent in excavating cavities in living pine trees (Conner and Rudolph 1995a). As discussed in Chapter 3, there is a great deal of variability in excavation length, often within the same stage of excavation in the same tree species and cavity population. Variation in physical constraints to excavation is not sufficient to explain the variation in the duration of excavation of different cavities. As cavities may sit idle for years before they are finally excavated to completion (Conner and Rudolph 1995a, Chapter 3), effort on the part of excavating woodpeckers is also likely affecting the length of the excavation process (see Chapter 3). In Part I it was postulated that effort may be a response to the need for new cavities to replace cavities that have been lost. Although some indirect evidence supported this hypothesis, a direct test was not possible. In Part II, this hypothesis and others relating to the strategies underlying the addition of new cavities to territories are tested directly. Specifically, three broad relationships are explored. First, the construction of new cavities at the group level is related to the availability of already existing cavities and to the loss of cavities from a territory. Second, an adult individual's contribution to excavation in a group is examined as a function of the individual's social status. Finally, the contribution of fledglings to excavation in relation to their future status as members of a group is examined. Hypotheses concerning these relationships are outlined below and are summarized in Table 6.1.

Red-cockaded woodpeckers typically live alone or in groups of two or more individuals (Walters et al. 1988). One to three helpers, most frequently young males retained from previous years, may share group membership with a breeding pair. Groups live on territories that are variable in size (Walters 1990). Territories contain both habitat for foraging and trees in which

cavities have been excavated (Walters 1990). The use of cavity trees by the woodpecker group defines what is known as the cluster (Walters 1990). A cluster may shift in space within a territory through the abandonment or reoccupation of old cavities and through the addition of new ones (Walters et al. 1988) through excavation.

The length of cavity excavation by the red-cockaded woodpecker represents a dramatic contrast to excavation by other North American woodpeckers, which excavate cavities in snags within two to six weeks (Conner et al. 1975, Conner and Rudolph 1995a). As a result, excavation behavior by red-cockaded woodpeckers is subject to very different selective pressures than that of its congeners. Both breeders and helpers are known to contribute to excavation (Ligon 1970). Given the length of time required to excavate a cavity (Conner and Rudolph 1995a, Chapter 3) and the variability in group membership between years (Lennartz et al. 1987), an individual excavating a given cavity may not eventually occupy that cavity (Baker 1971). The individual may suffer mortality prior to the cavity's completion, or may disperse to another territory. Excavation thus appears to be characterized by altruism, as individuals may make significant contributions to excavation of cavities which are then occupied by other individuals. This is intimately connected to the lag between commencement and completion of excavation, which makes the process of cavity construction one driven by future payoffs, rather than by current benefits. Interestingly, individuals may excavate at more than one cavity at a time (Walters, pers. comm.), and more than one individual may contribute to the excavation of a single cavity (Baker 1971). It is thus common for more than one cavity to be under construction at one time by one or more individuals on a given territory (Walters, pers. comm.).

Cavities are critical to red-cockaded woodpecker survival and reproduction, and must be replaced if they are usurped, lost, or abandoned. Two strategies relating to the excavation of new cavities suggest themselves. Given the high time cost of excavation, the addition of new cavities to a territory may be a form of bet-hedging involving the construction of surplus cavities in the event of future need. Alternately, the woodpeckers may be excavating cavities to a specific stage so that they can be completed quickly when the need arises (Chapter 3). Excavation may thus be a response to the more immediate need for new cavities. I seek to distinguish between these strategies by testing between them at two levels: that of the woodpecker group and that of the individual woodpecker.

In comparing strategies at the group level, I use the relationship between excavation and the immediate need for new cavities as a test. I postulate need to be related to the availability of cavities, expressed as the number of cavities relative to the number of individuals on a territory (cavity availability hypothesis). Given the potential variability in group composition over time (Lennartz et al. 1987) resulting from mortality and dispersal and from the recruitment of new helpers, as well as the fact that the cavities may be used intermittently over the years (see Chapter 4), there is likely to be variation among groups in the number of available cavities. Need may also be a function of the rate of loss of cavities on a territory (cavity loss hypothesis), which can occur through tree death and through enlargement of cavities by other woodpecker species to the point that they are rendered unsuitable to red-cockaded woodpeckers (Carter et al. 1988, Chapter 5). If an immediate need for new cavities is the mechanism underlying excavation at the group level, then excavation for a group as a whole is expected to be greater on territories characterized

by a cavity loss rate greater than zero cavities per year, or by a cavity to bird ratio less than one. The lack of such a pattern would support the alternate strategy of bet-hedging (bet-hedging hypothesis). Because the latter hypothesis is not tested directly, and because other plausible explanations may exist, such an interpretation would not be conclusive.

In seeking to distinguish between strategies of excavation at the individual level, I hypothesize that excavation by adults is mediated by social status. Social status appears to be responsible for a specific pattern of cavity occupancy. Roosting in cavities is mediated by a hierarchical system (Jackson 1994) in which dominance is determined primarily by sex and secondarily by age. Males (including fledglings) are dominant to females, and, within sexes, age and rank are positively correlated. Under this system, the breeding male normally resides in the highest-quality cavity on the territory (Walters, pers. comm.). Likewise, higher-ranked individuals appear to roost in cavities of better quality than do lower-ranked ones, and, if any individual lacks a roost cavity it is invariably a low-ranking bird (i.e. a female or a fledgling, Walters, pers. comm.). Patterns of cavity occupancy tend to be dynamic, however (see Chapter 4). As the average period of use of an individual cavity has the potential to exceed the lifetime of more than one bird (Conner and Rudolph 1995a, Chapter 4), and as group composition may be temporally variable (Lennartz et al. 1987), a turnover of individuals may be associated with residency in a given cavity.

Transitions in cavity occupancy also occur on a finer temporal scale. Once a new cavity is completed it is typically occupied by the breeding male, and this may trigger a reshuffling of roosting locations among other group members (Walters, pers. comm.). Given the system of dominance, it is also reasonable to assume that the breeding male will usurp the highest quality cavity on the territory should his own cavity fail (Walters, pers. comm.). This might then cause rearrangements in cavity use among other group members. I hypothesize that, if excavation is a response to the immediate need for new cavities, then those individuals most likely to be affected by cavity loss will make the greatest contributions to cavity excavation within their group (low-rank in need hypothesis). Low-ranked individuals have the greatest probability of being affected by cavity loss: (1) loss of the cavity of a higher-ranked individual may lead that individual to usurp the cavity of the low-ranked individual; and (2) loss of the cavity of the low-ranked individual leaves that individual without a cavity and without the opportunity of usurping a cavity. The contribution to excavation of an individual is therefore expected to be inversely related to that individual's rank in a group. However, if no high-quality cavities are available to a high-ranking bird that loses a cavity, that individual would have to excavate in order to eventually create a new cavity for itself (high-rank in need hypothesis). The contribution to excavation of an individual is therefore expected to be directly related to that individual's rank in a group.

Alternately, if a bet-hedging strategy is being followed, the contribution to excavation would be greatest by those individuals most likely to benefit from the cavity in the future, namely those most likely to occupy, or whose offspring are most likely to occupy, the cavity when it is completed (bet-hedging hypothesis). These probabilities are related to an individual's likelihood of sustaining residence on a territory. Whereas breeding males exhibit a high degree of territory fidelity, breeding females may disperse to other territories (Walters et al. 1988, Daniels 1997). This often occurs in response to death of the breeding male, and sometimes occurs even in intact groups (Walters et al. 1988, Daniels 1997). Helpers may occupy breeding vacancies on natal or

on neighboring territories (Walters et al. 1988). In groups with two helpers, older helpers are more likely to occupy a breeding vacancy than are younger helpers (Walters, pers. comm.). The greatest contribution to excavation within a group is thus expected to come from the breeding male, followed by the breeding female and a helper, with the youngest helper excavating the least.

The contribution of fledglings to the excavation process is not expected to be as significant as is that of adults. Fledglings are inexperienced excavators and may thus be subject to different selective pressures than are adults. Fledglings are therefore excluded from the above hypotheses and are considered separately. Following the breeding season, some fledglings maintain residency on their natal territory, whereas others disperse (Walters et al. 1988). Although very few female fledglings delay dispersal, the proportion of males delaying dispersal is twice that of those dispersing (Walters et al. 1988). I hypothesize that excavation on the part of fledglings is operating through one of two strategies. Excavation may be determined by whether a fledgling will delay natal dispersal following the breeding season. Alternately, excavation may be fulfilling a learning function by allowing a fledgling to gain experience. If a fledgling's dispersal decision does play a role, then a fledgling choosing not to disperse may gain from the addition of cavities to its natal territory (philopatry hypothesis). Those fledglings delaying dispersal are thus predicted to make the greater contribution to excavation. If the function of excavation is instead to gain experience, then no such pattern is expected (learning hypothesis). The same prediction is made if fledglings have not made a decision concerning dispersal at the time that they contribute to excavation (indecision hypothesis), so that the two hypotheses are not mutually exclusive.

The above hypotheses are tested by quantifying excavation by red-cockaded woodpeckers as a function of both the proportion of time they devote to excavation and the rate, measured in pecks per minute, at which they excavate. Describing and explaining these patterns is important to understanding the basic effect that the woodpecker's social organization has on the excavation process. More significantly, it is necessary for the formulation of even larger questions concerning the evolution and maintenance of both. In the shift toward inclusion of delayed dispersal as a life strategy in the red-cockaded woodpecker, the increase in group size resulting from retention of fledged young must have affected the dynamics of the excavation process. Larger groups would have required greater numbers of cavities, and a larger workforce would simultaneously have been available for their excavation. The presence of greater numbers of cavities on certain territories may have in turn selected for increased retention of young on those territories. This would have subsequently acted to contribute to an increase in the frequency of natal philopatry. This hypothetical scenario illustrates the possibility of a dynamic, reciprocal relationship between the process of cavity construction and the woodpecker's social system. The possibility of such a relationship underscores the fact that an understanding of the cavity excavation process or of the bird's social organization cannot be complete without an understanding of both.

TABLE 6.1. Hypotheses and predictions about the excavation process in red-cockaded woodpeckers.

Class of Hypotheses	Hypothesis	Mechanism	Predictions
Excavation at the group level	Cavity Availability	<i>Need:</i> the excavation process is a function of the immediate need for new cavities	Greater excavation on territories with a cavity to bird ratio greater than one.
	Cavity Loss	<i>Need:</i> the excavation process is a function of the immediate need for new cavities	Greater excavation on territories with a rate of cavity loss greater than zero
	Bet-hedging	<i>Bet-Hedging:</i> the excavation process involves the construction of surplus cavities	No evidence of the above patterns
Excavation at the individual level	Low-rank in need	<i>Need:</i> low-ranked birds drive the excavation process in seeking to minimize the cost of cavity failure to themselves or in seeking to move into a cavity of better quality	Breeding female, younger male helper, older male helper, then breeding male will make the greatest contribution to excavation
	High-rank in need	<i>Need:</i> high-ranked birds drive the excavation process in seeking to move into a cavity of better quality	Breeding male, older male helper, younger male helper, then breeding female will make the greatest contribution to excavation
	Bet-hedging	<i>Bet hedging:</i> those birds most likely to sustain residence on a given territory drive the excavation process, as the addition of cavities to that territory may benefit them in the future	Breeding male, breeding female and older male helper, then younger male helper will make the greatest contribution to excavation
Excavation by fledglings	Philopatry	Fledglings contribute to the excavation process in order to help construct cavities	Greater contribution to excavation by non-dispersing male fledglings
	Learning	Fledglings contribute to the excavation process in order to gain excavation experience	Equal contributions to excavation by all fledglings
	Indecision	Fledglings have not yet made a decision concerning dispersal at the time they contribute to excavation	Equal contributions to excavation by all fledglings

Methods

Study Area

The study was carried out over a period of two years on red-cockaded woodpeckers in three completely banded populations in North Carolina. Sampling was conducted in 1994 on two coastal populations on Camp LeJeune Marine Base (CL) and on the Croatan National Forest (CNF) between early July and mid-August. In 1995, woodpecker groups on Fort Bragg Military Reservation (FB), in and around the town of Southern Pines (SOPI) and on Camp Mackall (MACK) in the North Carolina Sandhills were sampled between late June and mid-September. The 'Study Area' section of Chapter 2 contains detailed descriptions of the study sites.

Data Collection

Criteria for Inclusion of Woodpecker Groups into Sample

A total of 46 woodpecker groups were sampled during the two years. I define a group as all of the breeders, helpers and fledglings affiliated with a territory during the breeding season, and use the words 'territory', 'site' and 'cluster' interchangeably. Seventeen groups consisted of a breeding pair, 17 had one helper and 11 had two helpers. One group originally believed to have two helpers was later determined to have three. This group was not included in the analyses. Each group had successfully fledged one or more young of either sex at least seven days prior to being sampled. In addition, each had at least one tree with one or more active or possibly active cavity starts, as defined in Chapter 2. Unless otherwise noted, starts refers to all non-completed cavities, including substarts and advanced starts. Sites with what was deemed an excessive number of starts exceeding 20 cm in depth just prior to the sampling period were not included in the sample, because visual observation of excavating birds was difficult at these starts (see 'Sampling Protocol' section below and 'Excavation Behavior' in the Results section). Despite these precautions, excavation of deep, or advanced, starts was witnessed at three of the sampled sites.

Data on the identity and status of all woodpeckers and on the activity status and stage of excavation of every woodpecker cavity in the study areas were obtained through cavity updating and population monitoring efforts that were part of long-term studies of this species (see Chapter 2).

Sampling Protocol

Data collection at each site took the form of instantaneous recording during scan sampling of starts and of continuous recording during focal sampling of excavating birds. Scan sampling yielded data on the identity of excavating individuals and served to quantify time spent excavating. These data were used to construct an excavational time budget for each bird, described in the 'Data Analysis' section. Focal sampling allowed the quantification of rates of excavation for different individuals.

Scan sampling of starts was used rather than focal sampling of starts in order to maximize the amount of data collected. As red-cockaded woodpeckers spend long periods of time away from their cavity trees during the day (Jackson 1994), focal sampling would include long periods of time spent at unattended cavities. Scan sampling was facilitated by the use of a hand-held spotting scope mounted on a rifle stock to locate excavators at a distance. A sampling path circumscribing entire groups of cavity trees was employed in most cases in order to reduce the probability of disturbing excavating birds. This procedure added significant amounts of time to each scan sample. Scan sampling duration thus ranged from less than one minute to as long as 20 minutes among sites, with most of the variability being due to differences in the physical location of starts relative to one another.

Any red-cockaded woodpecker seen at a start was assumed to be excavating and was identified using a second scope mounted on a tripod. Of 90 excavation events witnessed during both field seasons, only 63.3 % resulted in the successful identification of the excavating individual. Unsuccessful identifications were most frequently the result of a bird's flushing from a start and flying into the distance before I had the opportunity to read its bands. This was presumably a response to my presence. At times light conditions also interfered with my ability to identify an excavating bird. Because of the relatively high percentage of excavation events attributable to unidentified birds during the 1994 field season (33.3 %), an effort was made in 1995 to improve the probability of successful identifications by using a higher-powered Questar telescope and by increasing the sampling distance between myself and the starts. Despite these measures, an even higher percentage of excavating birds (37.3 %) remained unidentified in 1995.

Excavating individuals that were successfully identified became the subjects of focal observations. At times individuals were not at a start at the moment of scan sampling but were known to be in the vicinity of trees with starts. If these individuals began excavating within 5-10 min of the end of the scan sample, they were subjected to focal sampling, even though they were not counted as excavating in the individual's time budget calculation. Focal observations were conducted using a telescope mounted on a tripod. No blinds were used, but I was careful to keep a reasonable distance between myself and the focal individual. This distance was estimated in 1995 as averaging 110 meters, ranging between approximately 69 and 178 meters for 18 starts. No estimates are available for 1994, although the distances tended to be shorter.

Focal observations yielded information on the total number of excavational pecks to one or more starts and on the duration of excavation. Data on individuals excavating at advanced starts did not include the number of excavational pecks. Data were recorded by means of a hand-held microcassette recorder and transcribed at the end of each field day. They were then used to calculate mean peck rates for each individual, as described in the 'Data Analysis' section. Quantification of the total number of pecks was accomplished by counting pecks directly during excavation by an individual. I relied on visual contact with focal individuals in order to do this, as I was generally too far to hear. Because the woodpeckers excavate fairly quickly, the resulting peck numbers are to be regarded as reasonable estimates, rather than as precise values. As my counting was facilitated by the tendency of red-cockaded woodpeckers to excavate in short bouts separated by frequent pauses (see 'Excavation Behavior' in the Results section), the resulting data are reasonably accurate.

All observations ceased after one hour or when the focal individual completed an excavation session. This occurred when the individual left a start and flew into the distance. A bird exhibiting this behavior is unlikely to resume excavation in the immediate future, as it presumably has joined the rest of its group (Walters, pers. comm.), which may spend time on foraging forays some distance from where the cavity trees are located (Jackson 1994; Walters 1990). This could be inferred to have happened for certain individuals based on their vocalizations and on the vocalizations of their conspecifics. When visual contact with a focal bird was lost upon its departure from the start tree and no vocalizations were heard, it was difficult to determine whether the bird had left the immediate area. In these cases, observations were ended 15 min following its departure, unless the bird returned to a start within that period of time. I thus define an excavation session as the amount of time that an excavating individual spends at a start prior to suspending excavation for more than 15 min.

Rates of excavation may have been influenced to some degree by my presence. On occasion certain individuals appeared wary of me, hesitating to excavate or excavating slowly at first. Sometimes individuals moved away from a start upon my arrival, or even left a start tree for a period prior to resuming excavation. Individuals may sometimes have looked in my general direction or even directly at me while excavating. In general, however, most birds showing these signs appeared to habituate to me after an initial period of hesitancy.

Differences in Sampling Procedures Between Field Seasons

Some changes in sampling protocol were made between years. In 1994 each site was sampled 15 times. In 1995 sites were sampled an additional 15 times if excavation was detected, but dropped from the sampling rotation if it was not. Sites were dropped from the rotation in 1995 because I assumed that excavation was rare or was not occurring at all if it was not noted within the first 15 visits to a site. As a result, all sites were sampled throughout the study period in 1994, whereas there was a turnover of sites in 1995. Sites were sampled daily with the exception of several one to three day gaps and of one nine day gap. Not every site was sampled every day, and some sites may have been sampled twice in one day.

Whereas sampling in 1994 occurred over a 12-h period from early morning to early evening (0700-1900), it was limited to a 6-h period from early morning to early afternoon (0630-1300) in 1995. In addition, the time at which sampling began every day was thrice adjusted by 15-min increments in 1995 in order to compensate for changes in the time of sunrise. As a result of these differences, only those 1994 data collected during the times of day corresponding to the daily sampling period in 1995 were utilized in the analyses. This led to an uneven number of sample points per site in 1994 that ranged from eight to eleven.

Sample points resulting from daily scan sampling were distributed across three designated two-h time blocks categorized as early morning, mid-morning and late morning. Although their distribution was uniform in 1995, it was variable between sites in the preceding year. This may add some noise to the data if differences in excavation activity exist between time blocks.

Data Analysis

Cavity Excavation

Three variables relating to excavation were calculated for each individual belonging to the sampled groups. They were excavation time budget, mean excavation peck rate and excavation effort.

Excavational Time Budget. An individual's excavation time budget was calculated by dividing the number of excavation events for that individual by the number of times the individual's site was sampled. This calculation represents the proportion of time that the individual spent excavating during a 6-h period between early morning and early afternoon. As a proportion, this value is a dimensionless index with no unit of measurement (Martin and Bateson 1986). The calculation of proportion of time that groups spent excavating was based on the number of sample points for a site for which excavation occurred, regardless of the number of individuals excavating for each sample point. Two woodpeckers excavating simultaneously at a site were thus treated as a single excavation event for the group.

Because of the unsuccessful identification of some of the excavators in 66.7 % of excavating groups ($n = 27$) for both years, time budgets calculated for individuals must be regarded as relative values. There is no reason to believe that these values are biased toward certain individuals, however. In groups with helpers, the proportion of time spent excavating by the entire group accounted for by unidentified birds is relatively small. Although this proportion is relatively large in some of the groups with no helpers, the fact that breeders of both sexes were excavating in these groups suggests that these data are not biased toward the identification of a particular individual. The potential for bias in fact exists in only two groups in which only a single individual was consistently identified and in which unidentified birds accounted for a substantial proportion of the total excavation time for the group. Both groups were omitted from analyses involving excavation at the level of the individual.

The use of instantaneous recording may have resulted in an underestimation of the proportion of time that individuals spent excavating when these individuals were not seen at a start at the exact moment of sampling. When this happened, excavating individuals were not recorded as having excavated during that scan sample. In theory, these 'near misses' are balanced by the number of times that an individual *was* seen excavating when it could have been missed if the sampling had occurred at a slightly later time. In two instances, however, individuals that were observed excavating in near misses had 0 values for their excavation time budgets. This was also the case for seven other individuals on which focal observations had been conducted or which had been seen excavating during another individual's focal observation. In these cases, the individuals did not begin excavating until well after the scan sample had been completed. This problem is addressed in the Results section.

Another potential source of error in calculating time budgets may result from the sampling of advanced starts, as the starts may be deep enough that excavating woodpeckers may be concealed within them at the moment of sampling and thus be missed. My distance from the starts I sampled

was great enough that an excavating bird would not be heard. The majority of sampled sites had at least one advanced start. I sampled some of these starts more carefully by extending the length of the moment of sampling. I also walked up to a few of them where I had previously seen individuals excavating, so that any individual inside the start would flush out. In general, though, time constraints prevented me from treating all advanced starts in this way.

Differences between field seasons in the number of sample points per site may also affect the calculation of excavation time, as the value of a proportion resulting from a greater number of sample points may be more accurate than one based on a lesser number. A Mann-Whitney U test found no significant differences in the excavational time budgets of individuals between the two years for groups that excavated ($U = -0.1793$, $p = 0.858$). These time budgets included those of individuals that did not excavate. Despite the results of this test, the 1994 data have much greater variability than do the 1995 data (Table 6.2). Values for the two years were always compared prior to being combined for each analysis relating to excavation time.

Mean Peck Rate. A peck rate was calculated for each focal observation by dividing the total number of excavational pecks by the total time in minutes that the focal individual spent at a start. I define an excavational peck as a blow with the beak to the interior of a start. Pecks directed at the rim of a start were difficult to quantify as they were made erratically. Because of this, and because I was uncertain that their function was excavational, I did not include such pecks in the total excavational peck count. I define the total time that an individual spent at a start to include periods of inactivity during which excavation was not occurring. Red-cockaded woodpeckers sometimes pause from excavation for prolonged periods of several minutes while remaining stationary at a start. Differences in peck rates are thus a function of both the speed at which excavational pecks are made and the duration of periods of inactivity at a start.

A mean peck rate was calculated for each individual with at least two focal observations deemed reliable in estimating a peck rate. For those individuals with only one focal observation, the peck rate resulting from that observation was used in place of the mean peck rate. Observations were judged to be unreliable when I had trouble estimating the total number of excavational pecks. This occurred only when pecks were made erratically, rather than as part of well-defined bouts (see ‘Excavation Behavior’ in the Results section). Another problem stemmed from the fact that the rate at which pecks are directed at a start can vary within an excavation session. Because of this, short periods of excavation may be unreliable in estimating the peck rate for an entire session. Therefore, of a total of 73 focal observations, seven

TABLE 6.2. Mean excavational time budgets, representing the proportion of time spent excavating during a 6-h period, based on all adult red-cockaded woodpeckers in groups that excavated. Time budgets are reported for 1994, for 1995, and for both years combined. Individuals from two groups with biases in the identification of excavators were omitted.

Year	n	Mean	SD
1994	26	0.07	0.15
1995	48	0.02	0.04
Combined	74	0.04	0.09

observations in which the focal bird was at a start for less than five minutes were excluded from the analyses. Between one and four focal samples meeting reliability criteria were collected per excavating individual, with an average of two.

Peck rates for individual focal observations were compared between the two field seasons and found not to be significantly different ($t = 0.4216$, $p = 0.675$). Given this result, the data from both years were tested together in all subsequent analyses.

Excavation Effort. The excavational time budget of each individual was multiplied by that individual's mean peck rate to yield a measure that I call excavation effort, expressed as average pecks per minute over the 6-h period. This variable thus represents an individual's total contribution to excavation in its group as a function of the proportion of time that the individual spends excavating and of the rate at which it works when it is excavating. A more comprehensive measure would have included the average force with which pecks were delivered to a start, but this would be extremely difficult to quantify.

Excavation effort provides a more realistic estimate of excavation than does either time budget or peck rate alone. However, because it relies on these two variables for its calculation, the calculation is precluded if a value is missing for either of these variables. This turned out to be the case for three identified and several unidentified individuals observed excavating in scan samples but for whom peck rate data were unavailable. This problem is addressed in the Results section.

Cavity Availability and Cavity Loss

Cavity to bird ratios and yearly rates of cavity loss were calculated for each cluster for comparison with excavation effort at the group level. The null hypothesis predicting no differences in effort between groups was tested against the hypotheses that (1) groups affiliated with clusters with cavity to bird ratios less than one and (2) groups affiliated with clusters with rates of cavity loss greater than zero exhibit greater effort.

Two sets of cavity to bird ratios were calculated. Both were based on the number of cavities in a cluster that were considered to be suitable (see Chapter 5) and on the total number of birds in a group. This number included both adults and male fledglings in the first set, but only adults in the second. Female fledglings were not included in either calculation, as they are unlikely to sustain residence on their natal territory (Walters et al. 1988). The calculation of two sets of ratios was motivated by uncertainty as to whether male fledglings should be considered future occupants of cavities on their natal territory, given that they might exhibit either natal dispersal or philopatry. The ratios from each set were categorized according to whether their value was less than one or equal to or greater than one.

The rate of cavity loss for a cluster was based on the breeding season during which that cluster was sampled and on the year immediately preceding it. Loss of cavities occurs both through cavity enlargement by other woodpecker species and through death of cavity trees (see Chapters 2 and 5). The latter did not contribute to the loss of cavities in either year, as cavities on trees that died were either not completed, already enlarged, or relict cavities that had long been

abandoned. The rates were thus based entirely on the difference between years in the total number of enlarged, completed cavities in each cluster. Following their calculation, rates were categorized according to whether they were equal to zero or greater than zero.

Four clusters were omitted from the comparison of group excavation to rates of cavity loss, as information regarding death of cavity trees and enlargement of cavities was missing for them. An additional cluster was part of an unusual phenomenon involving an 'exchange' of breeders between it and other clusters in 1995. Because of the effect that this may have had on excavation (none was detected) in this cluster, it was excluded from all analyses and descriptive statistics.

Results

Excavation Behavior

I conducted approximately 46-h of focal observations on excavating birds in 1994 and in 1995. The following is a mostly anecdotal account, based on the focal observations, of red-cockaded woodpecker behavior relating to the excavation process.

I witnessed excavation under a wide range of weather conditions, including hot, cool, overcast, breezy and foggy weather. On one occasion the temperature was high enough that the excavating bird was holding its beak open when not pecking. I tended not to sample on wet days and therefore can not state with certainty that red-cockaded woodpeckers will not excavate during rainy weather. However, I did witness one individual suspending excavation as it began to rain, and another doing the same just prior to drizzly weather.

The majority of the excavation sessions I observed took place at starts, although I witnessed excavation at some substarts and advanced starts as well. The average duration of an entire excavation session could not be quantified as I could not determine how long an individual had excavated prior to the moment of sampling. Red-cockaded woodpeckers appear to be capable of excavating for more than one hour at a time, however, as some individuals were still excavating at the end of full, one hour focal observations. A woodpecker excavating at a start or at a substart does so from a vertical position, while perched on the trunk at the start opening. The angle of the body relative to the trunk is determined by the degree to which the individual has to lean forward and into the interior of the start in order to excavate. This is in turn dictated by start depth. Excavation at advanced starts thus requires that the body be positioned horizontally relative to the tree trunk. In these cases, the individual may be positioned almost completely inside the start.

Excavation at starts is characterized by pecking organized into clearly defined units which I refer to as excavational bouts. Each bout consists of a series of pecks delivered in rapid succession to the interior of a start. Less forceful pecks were sometimes directed at the lip of a start and, on one occasion, at the ceiling of a start. Each bout is separated from the next by a pause, during which a woodpecker returns its body to a fully vertical position at the start exterior. Pauses are generally brief, lasting one or more seconds, although pauses of several minutes did occur. Duration of bouts depends both on the number of pecks delivered and on the rate at which

pecks are delivered. The number of pecks per bout is variable, ranging from one to 103 pecks for both years combined, and averaging 12 pecks (Table 6.3). The rate at which pecks are delivered may also vary among bouts. Alternation between bouts and pauses is rather rhythmical, but was at times disrupted by short, unexpected bursts of pecking. Individuals were on occasion seen exhibiting what could be interpreted as an alternate excavational behavior. In these instances, the individual appeared to be engaged in a pulling, rather than a pecking, motion. This suggests that red-cockaded woodpeckers may sometimes remove pieces of wood still attached to a start's interior by tugging at them with their beak.

Excavation at substarts was observed only on a few occasions. In each case it was less rhythmic than excavation at starts in that it lacked clearly defined bouts. This may be a function of the shallow depth of a substart, which does not require a woodpecker to lean its body forward in order to excavate. As the need to alternate between a perching and an excavating stance is eliminated, so may be the need to pause with any regularity. Excavation at advanced starts, on the other hand, does involve the periodic return of the individual to a perching stance. When a start is deep enough, individuals have to back up out of the start in order to return to this position. As individuals at advanced starts are for the most part not visible when excavating, it is difficult to say whether excavation behaviors differ between advanced and shallower starts. One individual was observed spending up to 6 min at a time inside an advanced start (mean = 13.8 s, n = 3 focal observations). Bouts at advanced starts may thus be of greater length than bouts at other starts. It is unknown, however, whether an individual excavates the entire time when it is inside a start for an extended period.

Excavating red-cockaded woodpeckers exhibit a wide range of behaviors both related and unrelated to excavation. Among the former is the removal of wood chips from starts as a by-product of excavation. Although I have observed them falling out of starts during the excavation process, they apparently can accumulate in the start interior as well. Woodpeckers were observed removing wood chips by taking hold of several in their beak, resuming a perching stance at the start entrance, and shaking their head from side to side until all the chips had fallen. This behavior is likely the cause of the yellow 'spray' of wood chips sometimes seen sticking to the bark over a start. Alternate removal methods were also observed. One individual was seen scooping wood chips out of a start with its beak, while another was seen spitting a wood chip out. A third individual periodically shook its head from side to side in order to remove large wood chips that had stuck to its beak.

TABLE 6.3. Summary statistics of number of pecks per excavational bout in 1994, in 1995, and for both years combined. Sample sizes represent the total number of bouts. Data from focal observations deemed unreliable in estimating peck number were omitted from these calculations.

Year	n	Mean	SD
1994	6143	13.1	8.5
1995	10820	11.1	7.9
Combined	16963	12.1	8.2

Self-maintenance behaviors were also observed during pauses between bouts. They included preening, scratching, stretching of the wings, and wiping of the beak on the lip of a start. Foraging and excavation of resin wells at times occurred prior to or following excavation at a start, or during breaks from excavation during which the individual would leave the start. On several occasions, individuals were seen leaning back from their vertical position at a start during pauses from excavation. It was difficult to determine the purpose of this behavior, as I could not determine whether these individuals were looking upward or into the start interior at the time the behavior was exhibited. Another inexplicable behavior involved the opening and closing of the beak several times in succession. This behavior was exhibited by one individual at a start three times during the course of one focal observation, but was never seen again.

Red-cockaded woodpeckers appear to be vigilant and to actively interact with their surrounding environment while excavating. It was not uncommon to see excavating individuals surveying their surroundings, and on occasion responding to visual or auditory disturbances. A snorting deer, vocalizations by a flicker and territorial drumming by another woodpecker species all caused individuals to pause for a moment from excavation and to look toward the source of the sound. On one occasion an individual flew from a start immediately following a vocalization from a flicker. The responses described occur at a relatively low frequency, considering that the disturbances prompting the responses occurred on a daily basis in the study areas. Similarly, visible reactions to human-generated noises were few. Responses to loud explosions on the military bases and pauses in excavation due to approaching vehicles were each noted only during one focal observation.

Sometimes disturbances took the form of intrusions at a start by individuals of different woodpecker species. Of four interspecific interactions of this sort, two involved red-headed woodpeckers, one of which was an adult and one a juvenile, and two involved immature red-bellied woodpeckers. Each of the intruders landed at or near a start, causing the excavating individual to move away. On one occasion involving a breeding female, the excavating individual successfully displaced the intruder, and in another a female displayed aggressively toward the intruder until it left. In the latter case the female displayed displaced aggression in the form of forceful pecks to the tree and repeatedly approached the intruding woodpecker. On two other occasions, a helper and a breeding male each took evasive maneuvers and showed no resistance to the intruders. Interestingly, in one case these maneuvers involved moving to a nearby start on the same tree and excavating there until the intruder had gone. In the second instance, the individual moved up the trunk of the tree until the intruder left. One additional avoidance episode I witnessed involved an excavating breeding male leaving the tree altogether in response to a fox squirrel (*Sciurus niger*) moving up the trunk. The individual did not resume excavation within fifteen minutes of departing, despite the fact that the squirrel eventually left the tree. Although no conclusions can be drawn based on this anecdotal evidence, the possibility exists that an individual's sex may be related to that individual's ability to confront an intruder.

Interactions between excavating individuals and conspecifics were not uncommon, taking the form of vocal communication and of direct interactions at the start. Excavating individuals sometimes vocalized between excavational bouts, both on a sporadic and a consistent basis, throughout the focal observation. These vocalizations took the form of short calls and occurred

both in response to vocalizations by conspecifics and as part of vocal exchanges with conspecifics, although they sometimes appeared to be unprompted by either. An excavating individual was once seen responding to a vocalization from another red-cockaded woodpecker by flying from the start tree, and individuals were on occasion seen pausing briefly from excavation in response to a conspecific flying into the cluster. Direct interactions with other members of the group involved both adults and fledglings. The majority of these interactions resulted in the departure, sometimes temporary and sometimes permanent (within the context of the focal observation) of the excavating individual. Whereas fledglings would approach a start and leave shortly after the adult's departure, adults displacing an excavating individual would often begin excavating themselves. On one occasion three adult individuals were seen displacing one another at the same start. Two of them excavated at the start and the third excavated at resin wells.

Excavation sessions came to an end when the excavating individual left the start. Although at times the individual returned and resumed excavation within a matter of seconds or minutes, departures usually indicated that excavation was being suspended. Departure from a start took a variety of forms. Individuals were seen advancing up the trunk of the start tree, moving from a start prior to flying away and flying directly from a start. Some individuals flew to join the rest of their group immediately upon leaving a start, whereas others flew to an adjacent tree first. As I often lost visual contact with individuals just after they left a start tree, it is possible that some may remain in its vicinity rather than flying away.

Summary of Excavation Statistics

In all of the analyses that follow, the proportion of time that a group or individual spent excavating was transformed according to the arcsine-square root transformation. Whenever variances in the data were non-homogenous (Bartlett's test for homoscedasticity), analyses were conducted with untransformed data using non-parametric techniques.

Excavation Over Different Times of Day

The occurrence of excavation was compared between the blocks of time during which daily sampling was conducted. When the 1994 daily sampling period was divided into two 6-h blocks, (0700-1300 and 1300-1900), 77.4 % of all excavation events fell under the first block. This result only approached significance when the blocks were compared (Chi-square test, $X^2 = 3.040$, $p = 0.082$) despite the bias in sampling toward the first block (sampled 23 % more times than the second block). The first 6-h time block coincides with the daily sampling period for 1995. This time block was subdivided for each year into early morning (0630 - 0900), mid-morning (0830 - 1100) and late morning (1030-1300). Each of these blocks was 2-h long. The overlap between blocks is due to shifts in the time of sampling to account for differences in the time of sunrise in 1995. While excavation events occurred independently of time of day (i.e. 2-h time block) in 1995 ($X^2 = 1.297$, $p = 0.523$, $n = 675$ sample points), they did not in 1994 ($X^2 = 8.593$, $p = 0.014$, $n = 180$ sample points). The percentage of sample points for which excavation events were observed was higher in the early and late morning than in the mid-morning block of 1994 (Table 6.4). When the data for the two years were combined and excavation events compared across 2-h time blocks, the results were non-significant ($X^2 = 2.067$, $p = 0.723$, $n = 855$).

Excavation by Groups of Different Sizes

Excavation was more likely in groups with one- or two-helpers than in groups with no helpers (Figure 6.1; $X^2 = 8.069$, $p = 0.02$ for both years combined). The breeding male alone, the breeding female alone, or more than one bird including the breeding male or breeding female were responsible for the excavation observed in 52.6 % of groups with helpers ($n = 19$, does not include two groups with identification biases). In only 26.3 % of groups was a helper alone excavating (unidentified individuals were excavating in the remaining 21.1 %). The presence of a greater number of individuals in the larger-sized groups thus does not necessarily account for the greater percentage of those groups excavating.

TABLE 6.4. Percentage of sample points within each time block corresponding to excavation events in 1994, in 1995 and for both years combined. Sample sizes represent the total number of sample points for each time block.

Year	n	Early	n	Mid	n	Late
1994	60	23.3	56	5.4	64	10.9
1995	225	9.8	224	11.6	226	8.4
combined	285	12.6	280	10.4	290	9.0

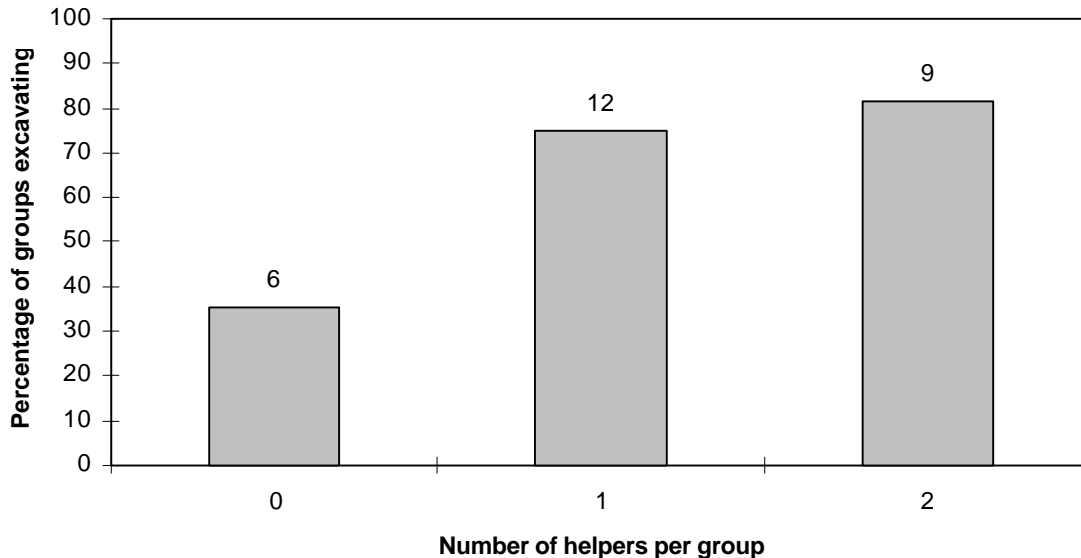


FIGURE 6.1. Percentage of groups for which excavation was witnessed within different group size categories (zero helper, one helper and two helper) in 1994 and 1995.

Excavation by Individuals of Different Status Classes

A total of 90 excavation events were witnessed involving 28 identified individuals and 17-27 unidentified individuals (depending on whether the same unidentified individuals were responsible for multiple excavation events). The identified individuals comprised only 33.8 % of all adults ($n = 77$) in those groups in which excavation occurred ($n = 25$, two groups with biases in the identity of the excavator omitted). The proportion of individuals excavating within each status class (breeding male, breeding female, helper in one-helper group, older and younger helper in two-helper groups) was compared across status classes in groups that excavated. Despite the fact that the proportion (expressed as a percentage) of younger helpers that excavated from two-helper groups was three times that of older helpers or single helpers (Table 6.5), differences among helper types were not significant ($X^2 = 1.603$, $p = 0.449$). All helpers were thus lumped into a single category. The proportion of individuals that excavated for both years combined was approximately equal for breeding males and helpers, but was lower for breeding females (Figure 6.2). Differences were not significant ($X^2 = 1.581$, $p = 0.454$), however.

Excavation of Different Cavities

Of the individual cavities upon which excavation was recorded on more than one occasion by identified individuals ($n = 13$), 23.1 % were excavated by more than one individual bird. This percentage may be higher in reality, as several unidentified individuals occurred in the groups with these cavities. Individual birds sometimes contributed to excavation of more than one cavity. The latter occurred only twice in 13 instances in which an individual was recorded as excavating on more than one occasion. However, in three of the instances, an unidentified bird excavated at a different cavity than the one at which the identified individual had excavated. It is possible that the unidentified and identified birds were the same individuals. The possibility thus exists in each of the three cases that the same individual excavated at two different cavities.

TABLE 6.5. Percentage of excavating individuals within each helper class for groups that excavated. The 'Helper' category refers to helpers in one helper groups. The remaining categories refer to helpers in two helper groups. Sample sizes represent the total number of birds sampled for each category. Data relating to two groups with biases in the identification of excavators were omitted.

Year	Helper		Older helper		Younger helper	
	n	%	n	%	n	%
1994	5	20.0	3	33.3	3	33.3
1995	6	50.0	5	40.0	5	0.00
Combined	11	36.4	8	37.5	8	12.5



FIGURE 6.2. Number of individuals that excavated and that did not excavate within different status classes in 1994 and 1995. Only individuals from groups that excavated are shown. Unidentified individuals that excavated are not shown.

Excavation Times

Individuals woodpeckers spent approximately one tenth of their time excavating in the 6-h daily sampling period (Table 6.6). Calculation of time spent excavating is based exclusively on those individuals that excavated in both years. The proportion of time that woodpeckers spent excavating was three times greater in 1994 than in 1995 (Table 6.6), a highly significant difference (Mann-Whitney U test, $U = 18.00$, $p = 0.003$).

The proportion of time that cavities were excavated by woodpecker groups was compared among groups of different sizes, both including and excluding those groups in which excavation did not occur. Analysis of variance found no differences between years within each group size category, and therefore the data from both field seasons were combined. Although significant differences existed between groups when non-excavating groups were included (Kruskal-Wallis ANOVA, $H = 7.186$, $p = 0.028$, $n = 44$), none did when non-excavating groups were excluded ($H = 1.102$, $p = 0.576$, $n = 27$). Two-helper groups exhibited the most excavation activity, approximately doubling that of one-helper groups (Tables 6.7 and 6.8), both when non-excavating groups were included and excluded. Differences among different-sized groups did not appear to be related to the presence of a greater number of excavating individuals in the larger-sized groups. Only three of 12 one-helper groups and one of 11 two-helper groups in which excavation was witnessed had more than one excavating bird (not including unidentified individuals).

TABLE 6.6. Mean excavational time budgets based on individual red-cockaded woodpeckers that excavated in 1994, in 1995, and for both years combined. Data from two groups with biases in the identification of excavators were omitted.

Year	n	Mean	SD
1994	8	0.22	0.20
1995	18	0.06	0.04
Combined	26	0.11	0.13

TABLE 6.7. Proportion of time that cavities were excavated by groups of different sizes in 1994 and 1995. Includes groups that did and did not excavate.

Group size	n	Mean	SD
No helper	17	0.04	0.07
One helper	16	0.10	0.12
Two helpers	11	0.19	0.25

TABLE 6.8. Proportion of time that cavities were excavated by groups of different sizes in 1994 and 1995. Includes groups that excavated only.

Group size	n	Mean	SD
No helper	6	0.12	0.07
One helper	12	0.13	0.13
Two helpers	9	0.24	0.26

Excavational Peck Rates

A total of 73 focal observations were conducted on 30 excavating individuals over the two field seasons. Of these, 59 observations conducted on 28 individuals were suitable for analysis based on the criteria outlined in the Methods section. For these individuals, peck rates ranged from 69.9 to 208.5 pecks/min (mean = 144.7 pecks/min) for both years combined (Table 6.9). Differences in peck rates between individuals with more than one focal observation were significant (one-way ANOVA, $F_{16,32,0.05} = 3.2647$, $p = 0.002$).

Average peck rates for individuals were compared among status classes. Mean rates for helpers in one-helper groups and older and younger helpers in two-helper groups were lumped into a single helper category after a Kruskal-Wallis ANOVA indicated no significant differences between them ($H = 2.000$, $p = 0.377$). Though no significant differences (one-way ANOVA, $F_{2,25,0.05} = 0.2816$, $p = 0.757$) existed in mean peck rates between status classes (Table 6.10), there was a significant difference among age classes (Kruskal-Wallis ANOVA, $H = 14.8069$, $p = 0.039$), which ranged from two to ten years (Figure 6.3). The means of the different age classes were compared using a nonparametric multiple comparison procedure outlined in Zar (1974, p. 200). The only significant difference found was between birds aged five and six years ($Q = 3.02$, $0.05 < p < 0.10$).

TABLE 6.9. Mean peck rates of red-cockaded woodpeckers in 1994, in 1995, and for both years combined.

Year	n	Mean	SD
1994	14	147.3	23.9
1995	45	143.9	27.2
Combined	59	144.7	26.3

TABLE 6.10. Mean peck rates of red-cockaded woodpeckers of different status for both years combined.

Status class	n	Mean	SD
Breeding male	11	148.3	28.0
Breeding female	9	143.0	15.8
Helpers	8	139.5	31.1

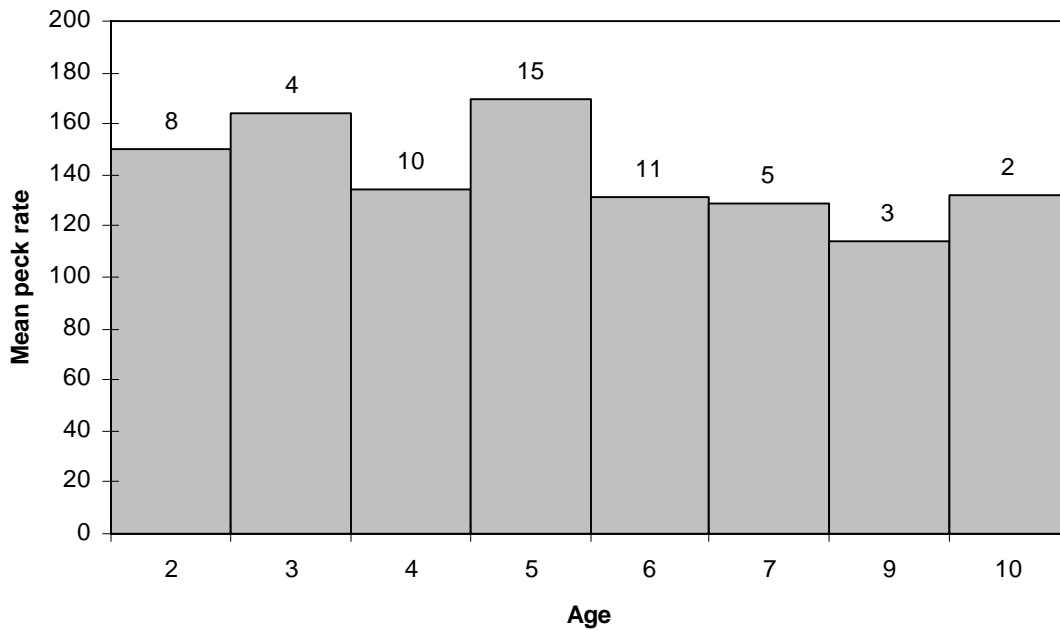


FIGURE 6.3. Mean peck rates of individuals in different age classes. Sample sizes refer to number of focal observations. Focal observations for individuals of ages 3, 9 and 10 were conducted on only one individual each.

Excavation at the Group Level

No significant difference between years existed in the proportion of time devoted to excavation by woodpecker groups (Mann-Whitney U test, $U = 224.5$, $p = 0.815$), so data from both years were analyzed together in all subsequent comparisons. Focal observations could not be conducted for all excavating individuals, so that excavation effort at both the individual and group level could not always be calculated. Thus, although peck rates did vary significantly between individual birds, the proportion of time spent excavating was used as a measure of excavation

activity. This proportion was used in place of excavation effort in testing both the group and individual hypotheses.

In a test of the cavity availability hypothesis, the proportion of time spent excavating by groups was compared between groups with different cavity to bird ratios. For those ratios that included male fledglings, means were greater for groups with less than one cavity per bird (Table 6.11) than they were for groups with cavity to bird ratios equal to or greater than one, as predicted by the hypothesis. However, variance was great for the former groups, and a one-tailed t-test indicated that differences between groups with different cavity to bird ratios approached significance ($t = 1.320$, $p = 0.097$). Omission of male fledglings from the ratios produced the opposite trend in the means among groups (Table 6.12), but differences between groups with different cavity to bird ratios were not significant ($t = -0.600$, $p > 0.72$).

The cavity loss hypothesis was also evaluated. While approximately 45 % of groups with no cavity losses did not excavate ($n = 29$), only 27 % of groups with cavity losses did not excavate ($n = 11$), suggesting a response to cavity loss. The hypothesis was tested directly by comparing the proportion of time spent excavating by groups with different rates of cavity loss. The mean proportion of time spent excavating was substantially higher in those groups with cavity loss rates greater than zero (Table 6.13), as predicted by the hypothesis. However, variability in excavation times was great, and differences between groups with and without losses were not significant (one-tailed t- test, $t = 0.910$, $p = 0.180$). Much of the difference in excavation times between groups with and without losses was in fact produced by a single group with exceptional activity (0.875). When this outlier was removed, both the mean and variability among groups

TABLE 6.11. Proportion of time that cavities were excavated by groups with different cavity to bird ratios, where ratios include male fledglings.

Cavity to bird ratio	n	Mean	SD
less than one	21	0.133	0.207
greater than or equal to one	23	0.069	0.094

TABLE 6.12. Proportion of time that cavities were excavated by groups with different cavity to bird ratios, where ratios do not include fledglings.

Cavity to bird ratio	n	Mean	SD
less than one	11	0.070	0.075
greater than or equal to one	33	0.110	0.179

TABLE 6.13. Proportion of time that cavities were excavated by groups with different yearly cavity loss rates.

Rate of cavity loss	n	Mean	SD
zero	29	0.088	0.123
greater than zero	11	0.139	0.252
greater than zero minus outlier	10	0.065	0.065

with cavity loss rates greater than zero were smaller than those of groups with cavity loss rates of zero.

An interaction between rates of cavity loss and cavity to bird ratios may be operating in those groups that had high excavation effort despite the availability of cavities or the lack of cavity enlargement on their territories. That is, a group may have a sufficient number of cavities per bird but may be losing cavities, so that the proportion of time spent excavating would be relatively high. In addition, a group may not be losing cavities but have an insufficient number of cavities, so that the proportion of time spent excavating would be relatively high. The presence of an interaction effect was tested by means of a separate two-way ANOVA for each cavity to bird ratio (with fledglings and without fledglings). The factors were cavity to bird ratio and cavity loss rate. The ANOVA for the ratio that included male fledglings yielded a significant result for the main effect of cavity to bird ratios ($F_{1,36,0.05} = 4.823$, $p = 0.035$), while the remaining results were not significant (cavity loss rate $F_{1,36,0.05} = 1.254$, $p = 0.270$, interaction $F_{1,36,0.05} = 3.032$, $p = 0.090$). Cavity loss thus appears to confound the effects of cavity availability on excavation effort by groups of woodpeckers. The ANOVA indicates that the proportion of time that groups excavated was influenced by the ratio of cavities to birds. However, when the group with unusually high excavation activity was omitted, the effect of cavity to bird ratio was no longer significant ($F_{1,35,0.05} = 1.761$, $p = 0.193$). A separate ANOVA was conducted using the cavity to bird ratio that did not include male fledglings. None of the results were significant (cavity to bird ratio $F_{1,36,0.05} = 0.191$, $p = 0.664$, cavity loss rate $F_{1,36,0.05} = 1.241$, $p = 0.273$, interaction $F_{1,36,0.05} = 0.405$, $p = 0.528$).

Cavity availability and rates of cavity loss for groups were further examined in relation to group size. The percentages of different-sized groups in which the ratio of cavities to birds was less than one were comparable between the three group sizes when male fledglings were included in the ratios, but was smaller in groups with helpers when fledglings were not included (Table 6.14). The need for cavities in relation to the availability of existing cavities thus could not explain the pattern of a greater percentage of groups with helpers excavating than groups without helpers (Figure 6.1; see also ‘Excavation by Groups of Different Sizes’ above). Cavity loss likewise appeared unrelated to this pattern, as the percentage of groups experiencing losses was comparable between groups with no helpers and one helper, while none of the groups with two helpers lost cavities (Table 6.14).

Additional factors may have affected excavation by groups. Territorial intrusions by birds unaffiliated with a group can disrupt breeding effort, as individuals in a group will spend time in conflict with these birds (Brust, pers. comm.). It is thus possible that the presence of these

TABLE 6.14. Percentage of different sized groups with cavity to bird ratios less than one (both with (a) and without (b) male fledglings) and with cavity loss rates greater than zero.

Group size	n	ratio (a)	n	ratio (b)	n	cavity loss
No helpers	17	47.1	17	35.3	17	17.6
One helper	16	43.8	16	25.0	16	25.0
Two helpers	11	54.5	11	9.1	7	0.0

floaters and intruders may also have a disruptive effect on other activities, such as excavation. The relationship between group excavation and presence or absence of floaters and intruders was examined. Only two groups were documented as having intruders or floaters. Excavation was not witnessed in either of them.

Excavation at the Individual Level

Contrary to what was predicted by the hypotheses of excavation by individuals (Table 6.1), the identity of excavating individuals varied both between and within woodpecker groups of different sizes. Both the breeding male and female excavated in one half of groups with no helpers ($n = 6$), while only one adult excavated in the other half (Table 6.15). In a test of the hypotheses, excavation time budgets were compared between the two status classes in those groups in which excavation by at least one identified individual was recorded ($n = 4$). Males spent more time excavating (mean = 0.07, SD = 0.04) than did females (mean = 0.04, SD = 0.03), but these differences were not significant (Mann-Whitney U test, $U = 5.0$, $p = 0.369$). The result does not support either the need or the bet-hedging hypotheses, which predict differences in excavation time budgets between status classes. However, as excavation by unidentified individuals in two of the groups accounted for 33.3 % and 50 % of the total time spent excavating by the group, the results are not conclusive.

In contrast to groups with no helpers, only one individual appeared to be excavating in the majority of groups with helpers (Tables 6.16 and 6.17), although unidentified excavators occurred in more than half of these groups (see below). Excavation by a single individual characterized 81.8 % of one helper groups ($n = 11$) and 87.5 % of groups with two helpers ($n = 8$). The identity of this lone excavator was highly variable between groups (Tables 6.16 and 6.17). Excavation by the breeding male, the breeding female and the helper alone was equally distributed in groups with one helper, while the identity of the excavating bird was unknown in three additional groups. In two helper groups, the breeding male alone excavated in two groups, the breeding female in one, the older helper in two, the younger helper in one, and an unidentified bird in one. Disregarding unidentified birds, multiple individuals excavated in only three groups with helpers: both the breeding male and a helper excavated in two of the groups, and the breeding male, breeding female and older helper in one other. The pattern of variability in the identity of the excavating individual in groups with single excavators does not support the bet-hedging hypothesis for excavation at the individual level (Table 6.1). Likewise, in groups with multiple excavators, the distribution of excavation time budgets does not correspond to

TABLE 6.15. Patterns of excavation in groups without helpers. Excavating birds are marked with an 'X'. Sample sizes refer to the number of groups exhibiting the respective pattern.

n	Breeding male	Breeding female	Unidentified Bird
1	X	X	
2	X	X	X
1	X		
2			X

TABLE 6.16. Patterns of excavation in groups with one helper. Excavating birds are marked with an 'X'. Sample sizes refer to the number of groups exhibiting the respective pattern. Data from one group with a bias in the identification of excavators were omitted.

n	Breeding male	Breeding female	Helper	Unidentified Bird
2	X		X	
2	X			
2		X		
2			X	X
3				X

TABLE 6.17. Patterns of excavation in groups with two helpers. Excavating birds are marked with an 'X'. Sample sizes refer to the number of groups exhibiting the respective pattern. Data from one group with a bias in the identification of excavators were omitted.

n	Breeding male	Breeding female	Older helper	Younger helper	Unidentified Bird
1	X	X	X		X
1	X				
1	X				X
1		X			
1			X		
1			X		X
1				X	X
1					X

the distribution predicted by the bet-hedging hypothesis (Table 6.18). Contrary to the prediction that the breeding male makes the greatest contribution to excavation, the breeding male in each group spent an equal or lesser proportion of time excavating than the helper.

The pattern of the single excavator in the majority of groups with helpers also does not coincide with the predictions of the low- and high-rank in need, which are based on distributions of time budgets of multiple excavators (Table 6.1). As higher ranking birds have the option of usurping a cavity, excavation by these birds suggests that no high-quality cavities are available. If no high-quality cavities exist on a territory, all individuals in a group would then be expected to excavate. A single excavator would be expected only if the lowest ranking individual were driving the excavation process. The presence of single, high-ranking individuals in many of the groups is thus inconsistent with the predictions. Furthermore, in the groups with multiple excavators, the distribution of excavational time budgets also does not correspond to those predicted by the low- and high-rank in need hypotheses (Table 6.18).

Unidentified excavators were found in over 50 % of all groups with helpers (n = 19). In four of these groups, only one excavation event was attributed to an unidentified excavator and no other birds were successfully identified. Only one individual was thus observed excavating, but

TABLE 6.18. Excavational time budgets of individuals of different status classes in groups with helpers and multiple excavators. The helper in CNF 27, a two-helper group, is the older helper.

Group	Breeding male	Breeding female	Helper
CL 20	0.10	0.00	0.40
FB 62	0.03	0.00	0.03
CNF 27	0.25	0.13	0.63

its status was unknown. Excavation by unidentified birds in the remaining groups may confound the single excavator pattern described above, however, as at least some of these birds may be different individuals than those who were successfully identified as excavating. Because the proportion of time that these birds spent excavating within each group was very low, the significance of their contribution to excavation for the group is questionable. This issue is explored below.

Primary Excavators

A set of criteria was developed to distinguish between those birds whose contribution to excavation was so minimal as to qualify them as incidental excavators and those birds making more regular or substantial contributions to excavation in their group. I term the latter ‘primary excavators’. Individuals that qualify as primary excavators have the following characteristics. First, they are responsible for at least 50 % of their group’s total excavation time in groups with no helpers, 33.3 % in groups with one helper, and 25 % in groups with two helpers; these percentages assume that all of the adults in a group contribute equally to excavation. Second, their individual excavation time is greater than 0.03, representing one sample point in 30 (where 30 is the maximum number of times any site was sampled), indicating that they may be excavating regularly.

The pattern of a single primary excavator of unpredictable status class being responsible for most excavation is very pronounced (Tables 6.19 - 6.21). Only two of six unidentified excavators to whom more than one excavation event was attributed were potential primary excavators. Thus, although nearly a third of all groups with helpers exhibited a pattern that diverged from that of the single excavator, only two groups, both with unidentified excavators, were characterized by multiple primary excavators. In addition, more than one third of all groups, including those with no helpers, had no primary excavators.

The phenomenon of the primary excavator may be an artifact of small sample size, in that the recorded contribution to excavation by an individual may be lower than its real contribution as a result of an insufficient number of visits to each site. In order to evaluate the effects of sample size, the temporal distribution of excavation events for a group was examined in relation to the identity of excavating individuals in those groups with more than one excavation event (n = 11, excavation attributable to unidentified excavators omitted). The first two excavation events for these groups were examined. It was hypothesized that, if the primary excavator phenomenon

TABLE 6.19. Patterns of excavation for primary excavators in groups without helpers. Excavating birds are marked with an 'X'. Sample sizes refer to the number of groups exhibiting the respective pattern.

n	Breeding male	Breeding female
2	X	
1		X
3		

TABLE 6.20. Patterns of excavation for primary excavators in groups with one helper. Excavating birds are marked with an 'X'. Sample sizes refer to the number of groups exhibiting the respective pattern. Data from one group with a bias in the identification of excavators were omitted.

n	Breeding male	Breeding female	Helper	Unidentified bird
1	X			
1		X		
2			X	
3				X
4				

TABLE 6.21. Patterns of excavation for primary excavators in groups with two helpers. Excavating birds are marked with an 'X'. Sample sizes refer to the number of groups exhibiting the respective pattern. Data from one group with a bias in the identification of excavators was omitted.

N	Breeding male	Breeding female	Older helper	Younger helper	Unidentified bird
1	X				X
1		X			
2			X		
1				X	X
1					X
2					

were not real, a random distribution of excavation events would exist in relation to the identity of the excavating individual. That is, two separate individuals would be recorded as excavating consecutively more frequently than the same individual would be. Assuming such a random distribution of excavation events, the average probability of recording a bird of a particular status excavating twice in a row would equal 0.36 for all groups combined. The probability of recording a bird of different status excavating after the first bird would equal 0.64. From these probabilities, expected frequencies of these two occurrences were calculated and compared to observed frequencies in a binomial distribution using a log likelihood ratio test for goodness of fit (G-test). The results were significant ($G = 6.007$, $p < 0.025$), indicating that the distribution of excavation events was non-random, but instead skewed toward recording the same individual excavating twice in a row.

Although the single primary excavator pattern does not appear to be affected by sample size, nine individuals who were never recorded as excavating during scan sampling were known to have excavated. All of the individuals belonged to groups with helpers. Five such individuals would not be assigned primary excavator status if the occasions on which they were seen excavating represented legitimate excavation events recorded during scan sampling. However, the remaining four woodpeckers were each seen excavating on more than one occasion, suggesting that their contribution to excavation may have been regular.

Excavation by Fledglings

No fledglings were identified as having excavated over the course of either field season during scan sampling. I did gather some anecdotal evidence of fledgling excavation, although it is open to interpretation. A total of five fledglings (four male, one female) were seen excavating following their displacement of an adult from a start. One of the males excavated on two separate occasions. An additional male fledgling was observed excavating without first exhibiting this displacement behavior. Of the fledglings, three excavated in 1994 and three in 1995. It is arguable whether excavation actually did occur in two of these cases, as the fledglings in question only pecked at a start or at the lip of a start a few times before departing.

Excavation by fledglings appeared qualitatively different than that by adults. Fledgling tended to peck in a tentative and erratic manner, although erratic pecking was on occasion exhibited by adults as well, especially when excavating shallow starts (see 'Excavation Behavior' section). Excavation sessions by fledglings also tended to be brief, normally lasting only a few minutes. One notable exception was a male fledgling on CL that excavated for approximately eight minutes. Quantification of a 166 second session by another male fledgling on CL yielded a peck rate of 39.2 pecks/min, well below the overall adult mean of 144.7 pecks/min. Based on these characteristics, it is difficult to determine whether fledglings were actually excavating effectively. That excavation by fledglings was relatively ineffective and that it often followed displacement of excavating adults by fledglings (suggesting that fledglings may have been observing adults excavating) suggests that excavation may be a learned behavior, or at least one that is honed through experience.

It is possible that I underestimated the frequency of excavation by fledglings to some degree, as some of the excavators that I was unable to identify may have been fledglings. I find this improbable, however, as I would expect to have seen fledglings among those excavators that were identified if fledglings do excavate with any frequency. This reasoning might not hold if there existed a differential response between adults and fledglings to the presence of an observer, such that fledglings would consistently flush from a start upon my approach. There are several reasons why this is probably not the case. The fledglings that I saw during focal observations on adults did not appear to be concerned with my presence. The reaction of fledglings to the presence of human beings, in fact, is generally based on the reaction of the adults in their group (Carter, pers. comm.). Fledglings generally stay close to adults, so that any solitary excavating individual that was not identified is not expected to have been a fledgling (Carter, pers. comm.). Finally, Carter (pers. comm.) reports only ever having seen a few fledglings excavating, and only during the wintertime, in the Sandhills population.

Discussion

Cavity Excavation

Cavity excavation by the red-cockaded woodpecker is a complex affair. Due to the mechanics of the process and to the highly social nature of the bird, excavation involves a rich array of behaviors that include interactions with conspecifics as well as with other cavity-dwelling species. The process itself is fraught with difficulties relating to the physical properties of the living pine trees in which excavation takes place, and as a result requires years to complete (Conner and Rudolph 1995a, Chapter 3). It is therefore surprising that, although there is a great deal of variation between both individual woodpeckers and woodpecker groups, the average amount of time devoted to excavation from day to day is very low. During the six hour period between sunrise and noon, individuals that excavate do so for approximately 10 % of the available time. Over 75 % of the woodpecker groups that excavated devoted 20 % or less of their time to excavation. Because excavation peaks during the post-breeding season period (Walters, pers. comm.) during which sampling was conducted, the amount of time that woodpeckers were recorded as excavating in this study is likely representative of their maximum excavation effort for 1994 and 1995. It is perhaps because a relatively small proportion of time is devoted to excavation that the process is so lengthy.

Whether the time that can be devoted to excavation is limited by some sort of constraint is unclear, as constraints are difficult to identify. Because all observations took place in the period following the fledging of new birds, the majority of time spent not excavating is presumably devoted to foraging (Jackson 1994), as well as to provisioning fledglings. It is difficult to determine whether a bird is constrained from excavating by the amount of time it must devote to foraging, as this time likely varies between territories with differences in foraging base. Another possibility is that the energetics of excavation act as a constraint on the maximum amount of time that can be devoted to it. Because the energetics of excavation have not been studied, it is unknown what the upper limits of a bird's endurance are in relation to this activity. The fact that a great deal of variation exists among individuals in the proportion of time they spend excavating, however, suggests that many individuals do not excavate to their full potential. Although it is plausible that differences in endurance exist between individuals, it is unlikely that such differences could account for the magnitude of the variation in excavation times between them (Table 6.6). Furthermore, because I rarely sampled the same site twice in one day, it is unknown whether excavation by an individual takes place in one session or can be intermittent throughout the day. If the latter were true, then constraints on excavation time due to energy expenditure are less likely.

Alternately, only small proportions of time may be devoted to excavation because the woodpeckers may be following a strategy that does not require them to excavate continuously. As discussed in Chapter 3, many territories are characterized by several non-completed cavities at various stages of excavation. The woodpeckers thus do not appear to be concentrating their effort on the consistent excavation of a single cavity, but instead are working slowly on many cavities. That relatively little time is invested in cavity excavation may be related to the fact that

cavities are used for many years following completion (see Chapter 4). The immediate need for a new cavity may thus not be too frequent. However, because excavation in living trees is prone to constraints, so that a cavity can not be excavated from start to finish quickly when it is needed, the strategy of working gradually on cavities that may be completed quickly when the need arises may be advantageous. Excavation appears to be at least partially related to need (see next section), which may help explain why excavation of individual starts proceeds irregularly over the years (see Chapter 3). The excavation of several starts on a territory may be a strategy to decrease the risk of losing cavities before the cavities are completed. Because cavity excavation requires a long time due to the physical constraints of excavating in living pine trees (see Chapter 3), non-completed cavities have ample opportunity to be lost through tree mortality or enlargement by other species. By excavating several starts in different trees on a territory, simultaneously or in a staggered fashion, there is greater probability of successfully completing at least one cavity over a long period of time than if the strategy were to invest all of one's excavation effort into a single start. Excavation may proceed on one start until sap flow reaches a rate that is intolerable or dangerous to a bird, and may then switch to another start.

It is also possible that the simultaneous presence of several starts on a territory is a byproduct of the construction of an individual cavity by each member of a woodpecker group. This does not seem to be the case, however, as (1) only one individual per group appears to be making substantial contributions to excavation (see following sections), (2) individual woodpeckers may excavate at more than one start on their territory, and (3) multiple individuals may excavate at a single start.

In addition to the fact that cavity excavation is lengthy, an important result arising from the analyses of duration of cavity excavation in Chapter 3 was that excavation length is subject to a great deal of variability. Whereas some cavities were completed from start to finish in only two years, others were still being actively excavated after 15 years. It was speculated that variation in the duration of excavation may be in large part due to variation in effort by excavating birds. The results of Part II confirm that variation in the time devoted to excavation is great. While certain individuals were recorded as excavating only 3 % of the time during the 6-hr sampling period, others spent over 60 % of the sampling period excavating. Variation was great at the group level as well, (Tables 6.7 and 6.8), largely due to variation in effort by single individuals in different groups. Variation in excavation effort thus likely plays a major role in determining the amount of time required to excavate a cavity. The mechanisms underlying variation in excavation effort are examined in detail in the sections that follow.

Excavation at the Group Level

In Chapter 3, variation in the number of birds available to excavate in a group was speculated to be a potential cause underlying variation in excavation effort. Based on the results of Part II, the time devoted by woodpeckers to excavation appears to be unrelated to group size when only excavating groups are considered, but is different in groups of different sizes when all groups that were sampled are included. Differences between groups of different sizes, however, are not a function of group size per se, as in the majority of excavating groups with helpers only one

individual excavated. The potential workforce available for excavation within a group thus does not appear to influence the time devoted to excavation by a group.

An alternative offered to the 'group size' explanation was that variation in excavation effort is a response to the need for new cavities as a function of cavity loss (see Chapter 5 and Table 6.1) or of the number of birds in relation to the number of available cavities (see Chapter 4 and Table 6.1). Based on the results of the tests of the hypotheses in this chapter, red-cockaded woodpeckers appear to excavate cavities at least partially in response to need. More specifically, the time spent excavating at the group level is, on average, greater on territories lacking cavities in relation to the number of woodpeckers available to occupy cavities. Although a response to cavity availability was in evidence when male fledglings were included in the total number of birds residing on a territory, it was not when they were excluded. This makes interpretation of the results less straightforward. Since male fledglings may exhibit either philopatry or dispersal (Walters et al. 1988) later in the season, it is unclear how they will impact cavity availability in a particular case. Most cavity updates are conducted in the pre-fledging period, so that data on cavity occupancy by fledglings are not collected. However, it is known that even fledglings that eventually disperse may occupy cavities for several months (Walters, pers. comm.), so that inclusion of fledglings in calculating cavity availability is reasonable. In addition, it is possible that cavity availability influences the decision of male fledglings to remain on their natal territory or disperse. Helpers reduce breeder workload in relation to incubation and provisioning of nestlings (Khan and Walters, 1997) and contribute to a higher production of fledglings (Heppel et al. 1994). Given the advantages of having helpers, excavation may partially be an attempt to retain male fledglings on a territory, therefore justifying inclusion of fledglings in the calculation of cavity availability even further.

Although not all tests of the hypotheses produced significant results, the results do represent trends that should not be dismissed. Groups in which cavity losses had occurred in the previous year spent a greater proportion of time excavating than groups that had not experienced losses. These trends are suggestive of a relationship between excavation and already completed cavities that is more complex than what was hypothesized. Groups with similar cavity loss rates may differ dramatically from one another in regard to the quality of their cavities, and birds within these groups may be responding directly to these differences. Excavation in response to need may be operating on multiple levels. Excavation may not only be a response to the availability of cavities on a territory, but to subtler mechanisms such as the gradual or long-term deterioration of cavity quality in addition to more instantaneous or dramatic losses. As discussed in Chapter 5, cavity quality may deteriorate as a result of reduced sap flow or runaway fungal heart rot, eventually leading to cavity abandonment. A bird capable of detecting changes in cavity quality may be tailoring the amount of time it excavates to these changes. A response to changes in cavity quality by individuals would in turn affect the proportion of time devoted to excavation by the entire group.

The results do not support the hypothesis that excavation is greater by groups that suffer the loss of cavities. The results do, however, support the hypothesis that excavation is greater by groups on territories where the individuals outnumber suitable cavities. At some level, then, groups appear to respond to the need for cavities with increased excavation. Knowledge of cavity

quality on the territories sampled is necessary to provide a more comprehensive picture leading to a reformulation of the hypotheses and to a fine-tuning of the categorization of woodpecker groups as being in or out of need. Such a re-categorization of groups would further be affected by the fact that patterns of cavity availability within groups may be more complex than those suggested by the simple cavity to bird ratios calculated in testing the hypotheses. Greater temporal variability than suspected may exist in patterns of cavity occupancy within groups of woodpeckers. The identity of individuals roosting in specific cavities was found to be variable within a seasonal period in a red-cockaded woodpecker population on Eglin Air Force Base in Florida (Haas and Walters, pers. comm.). At least some of this variability is a response to short-term usurpation of cavities by species such as southern flying squirrels (Walters, pers. comm.), which can occupy woodpecker cavities over consecutive days. The use of cavities by competing species may thus upset the established pattern of cavity occupancy by the group, even if on a short-term basis. If temporary usurpation of cavities is not uncommon, then intra-group competition for roost sites by red-cockaded woodpeckers may be frequent. Although such competition would certainly be mediated by hierarchical status, individuals flying in to roost earlier in the evening than other group members may have a competitive advantage in occupying and defending a cavity for the night. As discussed above, cavity availability appears to influence cavity excavation. Given the potential temporal variability in patterns of cavity occupancy due to cavity usurpation by other species, as well as by variability in group composition over time, patterns of cavity availability are likely complex and dynamic. Future studies should take these considerations into account in formulating hypotheses regarding group responses to the need for cavities.

Although it was not tested directly, the bet-hedging strategy of excavation seems unlikely. On a proximate level, the creation of surplus cavities would entail a genetic predisposition toward excavation that would operate independently of such external stimuli as the loss or unavailability of cavities. Such does not appear to be the case, given the results discussed above. That the premature excavation of cavities increases the probability of these cavities being enlarged or usurped by other species before they are even occupied by a red-cockaded woodpecker further argues against the construction of surplus cavities. Finally, the vast majority of cavities appear to be used by red-cockaded woodpeckers upon completion (Chapter 4). It is curious, however, that on more than one occasion during sampling, an individual was witnessed excavating at an advanced start situated on another group's territory. The individual was not identified in two of these instances, but was known to be a floater in the third. Although this suggests that the presence of non-completed cavities may provide a stimulus sufficient to misdirect a bird's excavation behavior toward cavities that it has no probability of occupying, other possibilities are equally plausible. In the case of the floater, the bird may have been trying to affiliate itself with a group by contributing to excavation or may have been trying to usurp a cavity from a group member.

Excavation at the Individual Level

This study confirms that, as observed by Ligon (1970), adult birds of all status classes excavate, be they breeders or helpers. As discussed above, even a floater was identified as excavating on one occasion. The contribution of fledglings to excavation, however, appears to be

non-significant. Despite the fact that adults of all social types can excavate, not all individuals available to excavate within specific groups do excavate. Excavation by red-cockaded woodpeckers often appears to be the responsibility of a single individual within a group, rather than that of multiple individuals. Furthermore, there is much variability between groups in the identity of this individual. The status class of primary excavators is variable and unpredictable in all group types (Tables 6.19-6.21). This pattern completely defies the predicted distributions regarding time devoted to excavation by individuals of different social status. The presence of single primary excavators in the majority of the groups counters the prediction of both need hypotheses, which are based on contributions by multiple group members directly or inversely proportional to their status (Table 6.1). Furthermore, variability among groups in the identity of the primary excavator contrasts with the prediction of the bet-hedging hypothesis that the individuals with the greatest probability of sustaining residence on a territory make the greatest contribution to excavation (Table 6.1). Based on these results, both the bet-hedging hypothesis and the two hypotheses relating to need are rejected in their present form.

Although it disqualifies the hypothesis relating cavity excavation to bet-hedging, the pattern of a single excavating bird is not completely at odds with the need hypotheses. It is clear that, at the group level, the need for cavities affects excavation. It is therefore likely that this relationship is present at the individual level as well. The variation among groups in the social status of excavating birds may simply be a function of which particular individual in a group is most in need. As discussed in the previous section, need may in turn be a function of the gradual deterioration in the quality of an individual's cavity, rather than of the sudden and complete loss of a cavity.

Under certain circumstances, the altruistic behavior exhibited by individuals excavating cavities they may not eventually occupy is not difficult to understand. Cavity excavation can require periods of more than a decade (see Chapter 3). Therefore, the probability always exists that an excavating individual may die or disperse prior to completing a cavity, and that the cavity may thus be occupied by another group member. Altruistic behavior on the part of the excavator in these cases can best be understood as incidental. Often the most recently excavated cavities become nest cavities and are roosted in by the breeding male. However, it appears as though over 40 % of nest cavities are not used as nests immediately following their completion, and many more are never used as nests (see Chapter 4). The implication of this finding is that the breeding male does not invariably occupy newly excavated cavities, at least not immediately. Thus, the probability of an excavating bird that is not the breeding male occupying a cavity it has excavated is greater, and the occurrence of altruistic behavior is less frequent, than what has been assumed.

More difficult to understand is the behavior of woodpeckers contributing to excavation of more than one cavity, which argues against incidental altruism. A relatively small percentage of individuals engaged in the such behavior. Perhaps inclusive fitness can be invoked as an explanation in these cases. As all group members stand to gain in fitness by the successful fledging of new offspring they are genetically related to, it is in the interest of all individuals in a group that high-quality cavities be available for nesting. In addition to excavation of cavities for themselves, individuals may thus contribute to excavation of what is to become the nest cavity.

However, as seen in Chapter 4, the need for nest cavities may not be a major factor influencing excavation, as newly excavated cavities that became nests were often not used as nests immediately. An analysis comparing use of cavities as nests to the availability of both old and new cavities would be necessary to determine whether preferences for new cavities for nesting exist. Equally puzzling is the displacement of excavating individuals by other members of a group, who then proceeded to excavate in their place (see 'Excavation Behavior' in Results section). It is in instances such as these that altruistic behavior becomes difficult to explain in light of modern adaptationist thinking.

Also difficult to explain is the presence of individuals that made irregular or insignificant contributions to excavation in approximately one third of the groups that excavated. It is hard to imagine the function that excavation might have in this context. It is also interesting that excavation appears to be more prevalent in groups with helpers than in those without, that is, that a higher percentage of the former excavated. In light of the single, primary excavator per group pattern, it is clear that group size is unrelated to the probability of witnessing excavation in these larger groups. Why excavation in these groups is more likely to occur is unknown.

Originally the interest in this study lay in identifying the mechanism responsible for differences in excavation between birds of different status under the assumption that all birds in a group contribute to excavation. In the process of seeking to answer this question, several puzzling trends and behaviors were uncovered. The question now focuses on identifying the mechanism that drives particular individuals within a group to excavate when others do not. Knowledge of the quality of the cavities on the territories sampled and of which individuals roost in which cavities is critical to providing a more comprehensive picture of the mechanisms underlying the social dynamics of cavity excavation in future studies.

Conclusions

The findings of this study provide strong empirical support for the ecological constraints model for the evolution of delayed dispersal in the red-cockaded woodpecker. The long times required for the excavation of cavities select for competition over breeding vacancies in already existing territories and against excavation of cavities in unoccupied habitat. Duration of cavity excavation varies between cavity populations, but may require over thirteen years in longleaf pine and over ten years in loblolly pine.

The length of the excavation process is subject to extreme variation. Much of the variation between pine species and cavity populations appears to center around the excavation of the start to advanced start stage. Explanations relating to differential sap flow and rates of red heart fungus infestation between species and cavity populations are unsatisfactory. As a great deal of variation in excavation duration also occurs within pine species and cavity populations, its most likely cause is variation in effort on the part of excavating woodpeckers. Field data confirms that such variation is great, and that it appears to be at least partially related to the need for new cavities in relation to the number of available cavities on a territory. It is likely that additional mechanisms are operating, e.g., individuals respond to deterioration in quality of their cavities through increased excavation. Interestingly, only a small proportion of an individual's time budget is devoted to excavation, which may contribute to the long duration of the excavation process.

Once completed, cavities are used for periods that may span more than fifteen years. Cavities are used for roosting immediately upon completion, and many are used for nesting within three years of completion. Duration of use varies between longleaf and loblolly pine. Cavities are used as nests for approximately six years in longleaf pine and three years in loblolly. Discontinuation of use of cavities for nesting is often permanent in both pine species. However, whereas cavities excavated in loblolly pine are abandoned altogether, longleaf cavities that are no longer used as nests are still roosted in for many years. Duration of cavity use in longleaf pine may thus triple duration of use of cavities in loblolly. Once completed, cavities excavated in longleaf pine are thus of greater value to the woodpeckers. Use of these cavities for roosting may be irregular between years, and more than one individual may roost in a cavity over that cavity's lifespan. Final abandonment of a cavity appears to be related to cavity loss.

Because of the length of the excavation process, not all individuals that contribute to excavation of a cavity will eventually occupy that cavity. Excavation behavior is therefore under selection by forces related to future, rather than to current, benefits. It was found that the majority of individuals devote little or no time to excavation. When excavation does occur, it is common for only one individual in a group to excavate. An even smaller number of these individuals make significant or regular contributions to excavation. Based on this pattern, the hypothesis that an individual's contribution to excavation is related to the probability of that individual eventually occupying a cavity was rejected. The pattern was likewise at odds with two hypotheses relating excavation to the need for new cavities. Given that the need for cavities is operating at the group level, individuals may be responding to need manifested at a level

undetected by this study. Future studies should incorporate data on the quality of cavities on a territory and the identity of the individual roosting in each cavity.

The length of time required to excavate cavities and the length of time that cavities are used upon completion confirm that cavities are a critical resource. The number of territories containing suitable cavities has in fact been linked directly to the number of woodpecker groups that a population can support. Quantification of the turnover of cavities in four cavity populations revealed that three of these (MACK, CNF and CL) are relatively stable in cavity numbers, but that a fourth (FB) has undergone declines over the past fifteen years. Cavity gains are thus barely keeping up with or are lagging behind cavity losses in these populations. Supplementation of existing territories with artificial cavities has contributed to a reduction in losses on FB and to net gains in the remaining cavity populations. Artificial cavities should continue to be used on FB in order to stabilize the cavity population and even bring about a positive balance in cavity turnover. On MACK, CNF and CL, artificial cavities are best used to induce the formation of new groups in order to expand the woodpecker population beyond the existing territories. Cavity restrictors should be used in all four cavity populations to help counteract cavity enlargement, which is a major force contributing to cavity loss. Of critical importance also is the protection of old-growth, as the woodpeckers will depend on a declining pool of such trees for cavity excavation until younger trees become suitable.

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Appendix

The missing measures of various tree and cavity variables were inferred for updates that were not conducted (update not taken) or that were not conducted during the breeding season (non-breeding season updates) in given years. Update not taken (UNT) refers to one or more consecutive updates. UNTs can also refer to updates that were conducted, but for which the measure of the variable in question was not recorded. Non-breeding season update (NBU) denotes that one or more pre- or post-breeding season updates were conducted, but no breeding season updates were conducted. What follows is a description of the protocol used to infer the missing measures for the different variables. Inconsistencies between updates of individual cavities (e.g., progression of stages of excavation out of order) were traced to the original field records and corrected.

Stage of Excavation (substart, start, advanced start, completed cavity)

UNTs following an update denoting a completed cavity represented completed cavities. UNTs preceding updates denoting a non-completed cavity represented non-completed cavities. If they preceded an update denoting a substart, the UNTs represented a substart. If they preceded an update denoting a start or advanced start, the UNTs represented a non-completed cavity of unknown stage. UNTs following an update denoting a non-completed cavity were handled as follows: (1) UNTs between two updates denoting identical stages represented non-completed cavities of that same stage; (2) UNTs between two updates denoting dissimilar stages represented non-completed cavities of unknown stage; and (3), UNTs following updates denoting a relict non-completed cavity represented non-completed cavities of that same stage, since non-completed relicts (see below) are rarely reactivated. UNTs between an update denoting a non-completed cavity and an update denoting a completely healed cavity represented non-completed cavities of the same stage as the earlier update. These UNTs were assumed never to have progressed beyond this stage, regardless of the number of years during which the cavity was not updated.

When NBUs were conducted, the missing breeding season update was treated as a UNT. The same procedures discussed above were thus employed to infer missing measures of excavation. In these cases, the update preceding the UNT may be a pre-breeding season NBU, and the update following the UNT may be a post-breeding season NBU. If a post-breeding season NBU denoted a cavity as being at a particular stage for the first time, the cavity was assumed to have already been excavated to that stage during that breeding season. If a post-breeding season NBU denoted a cavity that was a relict (see below), the cavity was assumed to have already been a relict of the same stage during that breeding season. When the first update for a cavity denoted that cavity as relict but did not provide information on the stage, the stage was assumed to be the same as that denoted by subsequent updates.

Cavities of questionable origin (possible starts) were assumed to have been of red-cockaded woodpecker origin if they were later classified as non-completed or completed cavities.

Activity (active, inactive, possibly active, relict)

As activity status of both completed and non-completed cavities is variable both within and between years, the specific activity of a cavity associated with a UNT could not be inferred, with one exception. UNTs denoting a nest cavity in a particular year were assigned active status during the breeding season of that year. Whether a cavity was or was not a relict cavity could be inferred, however. UNTs between updates denoting non-relict cavities represented non-relict cavities. UNTs following an update denoting a relict cavity represented relict cavities as well. There was one exception to this rule: if the UNT was followed by an update denoting that the cavity had been reactivated, the UNT represented a cavity of unknown activity status. UNTs also represented a cavity of unknown activity status if they preceded an update denoting a relict cavity, but were not themselves preceded by an update.

As was discussed in the previous section, the missing breeding season update was treated as a UNT when NBUs were conducted. If a post-breeding season NBU denoted a cavity as a relict for the first time, the cavity was assumed to have been a relict already during that breeding season.

Degree of Healing (partial, complete)

UNTs between updates denoting completed or non-completed cavities with the same degree of healing represented cavities with that same degree of healing. UNTs following an update denoting a cavity that was completely healed represented a completely healed cavity. UNTs between an update denoting a partially healed cavity and one denoting a completely healed cavity represented cavities of unknown healing status. If an NBU denoted a cavity as partially or completely healed for the first time, the cavity was assumed to have been healed to the same degree during that breeding season.

Degree of Cavity Enlargement (slight, moderate, great)

Enlargement can refer to enlargement of the entrance tunnel of a completed or non-completed cavity or to the cavity chamber of a completed cavity. The degree of enlargement of a cavity was not as important as whether the cavity was enlarged to a point where it was undesirable to a red-cockaded woodpecker. Cavities enlarged to a moderate or great degree were considered enlarged and undesirable, whereas cavities enlarged to a slight degree were counted as normal rather than enlarged in the analyses. UNTs following an update denoting an enlarged cavity represented enlarged cavities. UNTs represented cavities of unknown enlargement status if they preceded an update denoting an enlarged cavity, but were not themselves preceded by an update. If a post-breeding season NBU denoted a cavity enlarged for the first time, enlargement of that cavity was assumed to have already occurred by the breeding season. Enlarged cavities fitted with restrictors were considered not to be enlarged.

Status of a Cavity Tree as Living or Dead

UNTs between an update denoting a completed or non-completed cavity in a live cavity tree and an update denoting a dead tree represented cavities in tree of unknown status. However, if other cavities on the same tree were updated in the year of the UNT, the tree's status for that UNT was known. Death of a cavity tree recorded in a post-breeding season NBU was assumed to have occurred already by the breeding season.

Status of a Cavity as Having Broken or Not Having Broken from a Cavity Tree

Whether a completed or non-completed cavity represented by a UNT had broken from a tree could be inferred only under one specific set of circumstances for trees with more than one cavity. If a cavity that was updated in the year of the UNT was at a greater height on the trunk than the cavity represented by the UNT, then the status of the latter was determined as follows: if the updated cavity had not broken from the cavity tree, then the cavity represented by the UNT had also not broken. If a post-breeding season NBU denoted the breaking of a cavity, that cavity was assumed to have broken already by that breeding season.

Multiple Updates

Both completed and non-completed cavities were sometimes updated twice or even three times in one year, rather than just once. The updates chosen to represent the status of the cavity in those particular years were the following: (1) breeding season updates, if both breeding season and non-breeding season updates were conducted; (2) the last breeding season update to have been conducted, in cases in which multiple breeding season updates were conducted; and (3), in cases in which only multiple non-breeding season updates were conducted, the latest of the pre-breeding season updates or the earliest of the post-breeding season updates was used to infer breeding season status as described in the previous sections.

Common Cavities

In certain instances, two or more cavities were not recorded as a common cavity until several years after excavation on them had been completed. This may be a result of their common status having been overlooked during updating, but it could also represent a real change in their common status occurring over time as a result of cavity deterioration or of continued excavation of the cavity chamber by the woodpeckers. Cavities were assumed to have been common only in the years that they were indicated as such. An exception was made for cavities discovered as completed relict cavities and not recorded as a common cavity until later. Since relict cavities are not used by red-cockaded woodpeckers, it was assumed that these cavities had already been common when they were first discovered.

Cavities That are Lost-to-Follow-up

No information regarding any of the variables discussed above could be inferred for cavities for which UNTs included the last year of a study, except that cavities that were completed, relict,

completely healed, enlarged, on dead trees or broken in an update preceding the UNTs remained so.

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Animal Management Intern: September - December, 1991

Minnesota Zoo, Apple Valley, MN

Participated in zoo-keeping internship in the Southeast Asian Tropics Department. Duties included diet preparation and maintenance of animal holding pens. Designed and conducted short-term research project examining activity level responses of captive Indian flying foxes to increased food availability.

Animal Rehabilitation Intern: January - March, 1991

Chesapeake Wildlife Center, Bowie, MD

Participated in rehabilitation internship dealing with a variety of avian (shorebirds, passerines, raptors) and mammalian species. Veterinary duties included the handling and restraining of animals, the administering of injections and tube-feeding. Also helped organize manuscript detailing procedures for handling birds involved in oil spills.

Undergraduate Research: August 1989 - May 1990

Ross Park Zoo, Binghamton, NY

Conducted research on a group of captive Japanese macaques: explored the relationship between dominance and learning through experimental exhibit manipulation.

Teaching Experience:

Teaching Assistant, Ornithology Lab: January - April, 1997

Virginia Polytechnic Institute and State University, Blacksburg, VA

Teaching Assistant, General Biology Lab: January - April, 1995

Virginia Polytechnic Institute and State University, Blacksburg, VA

Presentations and Reports:

'The Social Dynamics of Cavity Excavation by the Red-cockaded Woodpecker', Animal Behavior Society Meeting, June 22, 1997

'The Dynamics of Cavity Excavation and Use by Red-cockaded Woodpeckers', co-authored report to Ft. Bragg, NC

'The Role of Delayed Benefits in Cavity Excavation by the Red-cockaded Woodpecker, *Picoides borealis*', report to Sigma-Xi, April 1996

Grants and Awards:

Sigma-Xi, the Scientific Research Society Grants-In-Aid of Research 1995

Alumni Association Graduate Fellowship Supplement, NCSU 1993