FEMALE DISPERSAL AND INBREEDING IN THE
RED-COCKADED WOODPECKER

by

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Female Dispersal and Inbreeding in the
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(ABSTRACT)

Dispersal is a critical life-history component; it determines gene flow and has profound effects on population structure, demography, social systems, and population viability. To add to our knowledge of dispersal and, in particular, our understanding of the relationship between dispersal and inbreeding, I studied three aspects of the biology of the red-cockaded woodpecker: dispersal of breeding females; the costs, benefits, and frequency of inbreeding; and the effect of inbreeding on natal dispersal.

Dispersal of breeding female red-cockaded woodpeckers is strongly associated with inbreeding avoidance and mate choice, weakly associated with site choice, and not found to be associated with social constraints. Estimates of mortality for non-dispersing and dispersing breeding females were 24 and 59 percent per year, respectively—rare evidence of the cost of breeding dispersal.

Significant costs of close inbreeding were found. Closely related pairs (kinship coefficient greater than 0.1) had lower hatching success as well as lower survival and recruitment of fledglings than unrelated pairs. Moderately related pairs (kinship coefficient between 0 and 0.1) and moderately inbred individuals had increased hatching success, but did not produce more young.

Despite documented costs of close inbreeding and a predictable spatial distribution of closely related males near the natal territory, female fledglings disperse a median of only two territories and a modal distance of one territory. Natal dispersal of females is affected by closely related males on the natal site but unaffected by closely related males or moderately related males that are off the natal site.

Dedication

To my mother, Ellen.

Acknowledgments

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CHAPTER 1: INTRODUCTION

Dispersal is a critical component of the biology of all taxa. By controlling gene flow, dispersal influences speciation and population structure (Wright 1977, Barrowclough 1980). Dispersal is intricately linked with demography and social systems (Shields 1982, Chepko-Sade and Halpin 1987), and has profound effects on population viability (Pulliam 1988, Harrison et al. 1988). Understanding the mechanisms of dispersal is vital to effective conservation in our increasingly fragmented landscapes (Walters in press). Thus, insight into dispersal behavior is important to a suite of biological disciplines.

In many species of wild animals, dispersal is affected by the presence of kin (Packer 1979, Pusey 1980, Shields 1982, Ralls et al. 1986). Movements of animals may reduce matings with close relatives (inbreeding avoidance; reviewed by Pusey and Wolf 1996) or increase matings with mildly related animals (optimal inbreeding; Shields 1982, Bateson 1983). In other species, no effect of kinship on dispersal has been found (Arcese 1989, Gibbs and Grant 1989). Increased knowledge of species-specific dispersal mechanisms is necessary to build a general theory of the ecological basis of dispersal strategies (Walters in press). To contribute to our slowly accumulating body of knowledge on dispersal and its relationship to kinship, I studied breeding dispersal, natal dispersal, and inbreeding in the red-cockaded woodpecker (*Picoides borealis*).

The red-cockaded woodpecker is an endangered, cooperatively breeding species endemic to the pine savannas of the southeastern United States. It is an excellent subject for studies of dispersal and kinship for several reasons: a) long-term data exist, which enable analyses not possible for most species; b) as a cooperative breeder, the species exhibits a complex dispersal pattern and increased opportunities for inbreeding; and c) the endangered status and fragmented distribution of this species impart an urgency to understanding its movements and potential sensitivity to close inbreeding.

This thesis contains five chapters. In this chapter, I introduce the subjects at hand, and describe the study species, study area, and methods of data collection. In Chapter 2, I examine the causes and frequency of breeding dispersal in the study population. In Chapter 3, I assess the costs, benefits, and frequency of inbreeding, and in Chapter 4, I investigate the potential effects of inbreeding avoidance and optimal inbreeding on natal dispersal. The final chapter, Chapter 5, summarizes my research.

BREEDING DISPERSAL

Breeding dispersal is the movement of individuals between successive breeding sites (Greenwood 1980), either within a breeding season (e.g. Jackson et al. 1989) or between breeding seasons (e.g. Korpimaki 1993). In most species of birds, breeding females disperse more frequently then do breeding males (reviewed by Greenwood 1980). Dispersal rates of breeding females reported in the literature include 45 to 52 percent for indigo buntings (*Passerina cyanea*, Payne and Payne 1993), 49 percent for red-winged blackbirds (*Agelaius phoeniceus*, Beletsky and

Orians 1991), 27.5 percent for eastern kingbirds (*Tyrannus tyrannus*, Murphy 1996), 18 percent for prairie warblers (*Dendroica discolor*, Jackson et al. 1989), and 12 percent for red-cockaded woodpeckers (Walters et al. 1988). By affecting gene flow and demographics, such movement or lack thereof has strong influence on population structure and viability (Payne and Payne 1993).

Presently, there are five hypotheses for the cause of breeding dispersal in birds: 1) breeding birds disperse to avoid inbreeding (inbreeding avoidance; Koenig and Pitelka 1979, Walters et al. 1988); 2) breeding birds disperse to find a better mate (mate choice; Payne and Payne 1993); 3) breeding birds disperse to find a better site (site choice; Payne and Payne 1993); 4) breeding birds disperse as a result of social constraints (social constraints; Payne and Payne 1993); and 5) breeding birds disperse because of genetic predisposition (heritability). To determine the causes of breeding dispersal in red-cockaded woodpeckers, I test the inbreeding avoidance, mate choice, site choice, and social constraints hypotheses (Chapter 2).

COSTS, BENEFITS, AND FREQUENCY OF INBREEDING

Inbreeding, or mating between individuals that share alleles identical by descent from a common ancestor (Crow and Kimura 1970), has documented costs and theoretical benefits. Loss of fitness due to inbreeding, or inbreeding depression, is most severe in highly inbred individuals of species that are adapted to large outcrossing populations (Lande 1988). Inbreeding depression is well documented in captive populations of animals (Ralls et al. 1979, Ralls and Ballou 1983), in experimental populations of *Drosophila* (Simmons and Crow 1977) and *Peromyscus* (Brewer et al. 1990, Keane 1990), and in domestic poultry (Schoffner 1948, reviewed in Woodard et al. 1982). Evidence of inbreeding depression in wild birds is scarce but slowly accumulating: inbreeding causes reduced hatching rates in great tits (*Parus major,* Bulmer 1973; Greenwood et al. 1978, van Noordwijk and Scharloo 1981), great reed warblers (*Acrocephalus arundinaceus*, Bensch et al. 1994), and blue tits (*Parus caeruleus*, Kempenaers et al. 1996), and reduced survival of song sparrows (*Melospiza melodia*) through severe weather (Keller et al. 1994).

Examples of the benefits of inbreeding are extremely rare (Pusey and Wolf 1996). Mating of individuals from distinct populations may disrupt intrinsically coadapted gene complexes or coadapted gene complexes supporting local adaptations (Templeton et al. 1986). Disruption of intrinsically coadapted genes has been documented in captive members of species with high rates of karyotypic inversions (*Gazella* spp., Ryder 1987; owl monkeys *Aotus trivirgatus*, de Boer 1982; *Drosophila,* Wallace 1991) while disruption of local adaptations has been shown in salmonids (Bams 1976, Altukhov and Salmenkova 1987, Reisenbichler 1988, Emlen 1991). However, the importance of outbreeding depression for wild birds and mammals remains unclear (Pusey and Wolf 1996).

In Chapter 3, I assess the costs of close inbreeding and the benefits of moderate inbreeding for red-cockaded woodpeckers. The long-term, ongoing study of a population of more than 500 woodpeckers has produced a data set of over 4000 marked individuals in 16 years. The pedigree constructed from these data is four generations deep, and yields over 20 closely related pairs, 50

moderately related pairs, and 700 unrelated pairs—unusually large sample sizes for a study of a wild population.

In addition, in Chapter 3, I calculate the frequency of inbreeding, and compare the observed frequencies with expected frequencies based on random pairing for three spatial scales: the entire population, four regions with the population, and small artificially constructed neighborhoods within one region. Comparing observed and expected frequencies of inbreeding has been used in the past to show a lack of inbreeding avoidance behavior (van Tierenden and van Noordwijk 1988, Gibbs and Grant 1989), but such an approach assumes dispersal throughout the population. By using three spatial scales for these analyses, I explore the confounding effect of dispersal patterns on analyses of this type.

NATAL DISPERSAL AND INBREEDING

Natal dispersal is the movement of individuals from their place of birth to their first breeding location (Greenwood 1980). Two factors which can affect natal dispersal are inbreeding avoidance (reviewed by Pusey 1987) and optimal inbreeding (Shields 1982, 1983).

Dispersal to avoid the costs of breeding with close relatives (inbreeding avoidance) has been reported for several species of birds and mammals, including olive baboons (*Papio anubis*, Packer 1979), acorn woodpeckers (Koenig and Pitelka 1979), chimpanzees (*Pan troglodytes*, Pusey 1980), black-tailed prairie dogs (*Cynomus ludovicianus*, Hoogland 1982), and Florida scrub jays (*Aphelecoma caerulescens*, Woolfenden and Fitzpatrick 1984). However, in these studies the cost of close inbreeding was assumed, and no previous studies have documented both the cost of close inbreeding and inbreeding avoidance for the same population or species.

Moderate inbreeding may provide benefits that promote the evolution of philopatry, or lack of dispersal (optimal inbreeding, Shields 1982, 1983). Very little evidence has been found to support this theory. Some species, such as Japanese quail (*Coturnix coturnix*, Bateson 1983) and white-footed mice (*Peromyscus leucopus*, Keane 1990), have been shown to prefer moderately related mates in laboratory settings. However, no study to date has linked inbreeding benefits with dispersal behavior in a wild population.

To reveal effects of inbreeding avoidance and optimal inbreeding on natal dispersal of red-cockaded woodpeckers, I first assess the spatial distribution of close and moderate relatives in the population. I compare this spatial distribution, or kinship structure, with the observed range of female dispersal distances, to detect whether dispersal distances serve to avoid close inbreeding or to promote moderate inbreeding. Next, I look for a change in the dispersal behavior of females in the presence or absence of related males.

THE RED-COCKADED WOODPECKER

CONSERVATION STATUS

The red-cockaded woodpecker is an endangered, cooperatively breeding species restricted to old-growth pine savannas of the southeastern United States. Before European colonization of Eastern North America, there were an estimated 1.6 million groups of red-cockaded woodpeckers continuously distributed across the southeastern coastal plain and Piedmont to eastern Texas and Oklahoma (Conner, Walters, and Rudolph in prep). This range closely coincided with that of the longleaf pine (*Pinus palustris*, Wahlenburg 1946), a species of pine preferred by the woodpecker for nest and roost cavities and for foraging (Jackson 1971). Longleaf pine was the dominant tree, and the red-cockaded woodpecker was one of the most common birds, in the fire-maintained savannas that once characterized the southeast (Wahlenburg 1946, Ligon et al. 1991). Today there are roughly 4500 woodpecker groups—less than one percent of the original number—scattered in small isolated populations in remnant patches of savanna (Conner, Walters, and Rudolph in prep). Although the species has been protected under the Endangered Species Act since 1973 (Ligon et al. 1991), its scattered populations continued to decline throughout the 1970's and 1980's (Costa and Escano 1989, Conner and Rudolph 1991, James 1991, Ligon et al. 1991).

The primary reason for the historical and recent declines is loss of the mature pine savanna required by the woodpecker (Ligon et al. 1986). Logging, conversion of land to faster-growing pine species and other agricultural products, fire suppression, and development have reduced the longleaf ecosystem to a few small, isolated remnants (Ligon et al. 1986, 1991, Conner and Ruldoph 1991). Recently, however, intensive management using prescribed burning (Ligon et al. 1986) and cavity enhancement (Carter et al. 1989, Copeyon 1990, Copeyon et al. 1991) has stabilized some woodpecker populations and induced increases as high as 5-10% per year in at least two others (Conner, Walters, and Rudolph in prep). We now possess the knowledge necessary to recover the species, although we may lack the political will to continue existing protection and to convert additional land to the mature longleaf required for the future existence of this species (Conner, Walters, and Rudolph in prep).

ECOLOGY

Red-cockaded woodpeckers are restricted to old-growth pines because of a life history characteristic unique among North American woodpeckers: they excavate nest and roost cavities in live pine trees. Only a mature tree can accommodate a cavity entirely within its heartwood, which is necessary to prevent potentially deadly sap from the outer sapwood from entering the cavity. In addition, older trees may be more prone to infection by red heart fungus (*Phellinus pini*), and cavities are more easily excavated in infected trees (reviewed by Rudolph and Conner 1991). Typically, trees over 80 years old are available for cavity use by red-cockaded woodpeckers (Delotelle and Epting 1988, Hooper 1988, Conner and Rudolph 1991). However, in studies of which tree age is preferred by woodpeckers for cavity trees, birds consistently choose the oldest available age class—even when extremely old trees (300 years and older) are present—and therefore, we do not yet know the optimum age for cavity trees (reviewed by Rudolph and Conner 1991). Among mature trees, older trees can accommodate cavities within the heartwood

at greater heights than younger trees, and increased cavity height may decrease predation, lower the risk of damage by fire, and decrease any harmful effects of excavation on the tree itself (reviewed by Rudolph and Conner 1991).

Excavation in live pines may have evolved because of a shortage of snags in the fire-maintained longleaf system. It also functions to lower predation: the birds exploit the sap flow in live trees by creating resin wells (wounds in the outer cambium) above and below the cavity, and the sap leaked by the resin wells effectively prevents predation by arboreal snakes (Rudolph et al. 1990). Longleaf pine is preferred, but loblolly (*P. taeda*), pitch (*P. rigida*), pond (*P. serotina*), shortleaf (*P. echinata*), and slash (*P. elliottii*) pines are also used (Jackson 1971). Longleaf pine may be preferred because it has greater sap flow than other pines.

SOCIAL SYSTEM

Cooperative breeding is a social system in which adults (helpers) assist conspecifics in raising young that are not their own (Brown 1978). In the red-cockaded woodpecker, such aggregations of adults are termed groups, and the set of cavity trees a group occupies is termed a cluster (Walters et al. 1988). Not all groups have helpers, nor do all birds help (Lennartz et al. 1987, Walters et al. 1988). In south-central North Carolina, roughly half of fledgling male red-cockaded woodpeckers remain on their natal territory to help raise subsequent years' young; the other half of fledgling males disperse and acquire a breeding position elsewhere or more rarely, help at a site other than their natal territory (Walters et al. 1988).

Females of the species rarely act as helpers (Walters et al. 1988), presumably because there is little chance of females inheriting the natal territory without risk of close inbreeding. However, the dynamics of female helping are complex: elevated rates of female helping in some populations have been linked to lower mortality of breeding females (Delotelle and Epting 1992). In all populations, breeding females exhibit higher mortality than breeding males (Walters et al. 1988, Delotelle and Epting 1992).

Cooperative breeding is exhibited by more than 300 species of birds and has clearly evolved in response to more than one set of ecological conditions (Walters et al. 1988). One commonly accepted ecological basis for cooperative breeding is unusually high variation in territory quality (reviewed by Koenig et al. 1992). For the red-cockaded woodpecker, this high variation in territory quality is manifested as suitable habitat with and without the critical resource of sufficient cavities (Walters et al. 1992). The cavity is a critical resource presumably because construction of cavities is an energy-expensive process taking one to several years to complete (Conner and Rudolph 1995).

POPULATION DYNAMICS

Cooperative breeders exhibit unusual population dynamics. The presence of helpers ready to fill breeding vacancies buffers the effect of changes in the mortality rates of breeders on population-level reproduction (Walters 1991). Such buffering increases population stability and persistence. However, population growth or decline in cooperative breeders is strongly dependent on the number of breeding groups (Walters 1991). Understanding and managing

factors that affect the number of breeding groups in the red-cockaded woodpecker is more important to the recovery of populations and the species than is the management of factors that affect adult mortality (Walters 1991).

One of the factors that affects the number of breeding groups in this species is movement of females. Males are remarkably site-faithful, in that many of the male fledglings inherit their natal territory, but also because breeding males rarely change territories (Walters et al. 1988). In contrast, females almost always disperse from their natal territory and often change breeding locations as adults (Walters et al. 1988). Dispersal of female red-cockaded woodpeckers is key to the maintenance of active groups and therefore the continued existence of a population.

THE STUDY AREA AND METHODS OF DATA COLLECTION

The study area is located in the Sandhills of south-central North Carolina, and encompasses over 110,000 ha. The dominant vegetation is second-growth longleaf pine, with an midstory of scrub oaks (Quercus spp.) and a ground cover of wiregrass (*Aristida stricta*). Pond pine is found in wetter sites, and loblolly pine and old-growth longleaf pine occur occasionally throughout the study area. Some sites are open savanna, while others contain a dense understory that results from fire suppression. The study area consists of four regions: Southern Pines (SOPI, 16400 ha.), which is privately owned lands including golf courses and horse farms; the Sandhills Game Lands (SGL, 16800 ha.), which is mainly undeveloped federal lands; Fort Bragg (FB, 12000 ha.), encompassing the western third of the Fort Bragg Military Reservation, contains much open savanna; and the minor sites (MIN, 69000), which are aggregations of groups loosely scattered throughout agricultural lands. All woodpecker groups within the study area (roughly 220) are monitored. Additional groups, not monitored by this project, occur to the south and east of the study area.

Data collection began in SOPI and SGL in 1980, in FB and MIN in 1981, and continues through the present. All individuals are banded with a unique color combination and reproduction of all groups is monitored. Most individuals are banded as nestlings, and each breeding season all members of each group are identified through the use of spotting scopes and nets, if necessary. Breeding status is assigned based on behavioral observations and/or the relative ages of birds present, and group affiliation is assigned through behavioral observations and roost checks. Sex is determined by the presence of a red crown patch in males during their first fall, or by the presence of the red cockade in adult males which is verified through capture. Through these data, parentage and placement of most individuals is known. Detailed descriptions of the study area and methods of data collection are given by Carter et al. (1983) and Walters et al. (1988).

CHAPTER 2: DISPERSAL OF BREEDING FEMALES

INTRODUCTION

The dispersal of breeding adults affects the population dynamics and genetics of many species of birds (Greenwood and Harvey 1982). Movement of adults can increase reproduction in a population; it can also provide gene flow and reduce inbreeding. Research into the possible causes of this important behavior has intensified over the past decade (e.g. Jackson et al. 1989, Part and Gustafsson 1989, Payne and Payne 1993, Murphy 1996, and others.) In this study, I examine over 240 between-year movements of breeding females within a large population of red-cockaded woodpeckers (*Picoides borealis)* in south-central North Carolina. Preliminary analyses of breeding dispersal within this population were presented by Walters et al. (1988); here I continue this work with a larger data set and in greater detail.

I test four adaptive hypotheses for the cause of breeding dispersal in red-cockaded woodpeckers: 1) breeding birds disperse to avoid inbreeding (inbreeding avoidance; Koenig and Pitelka 1979, Walters et al. 1988); 2) breeding birds disperse to find a better mate (mate choice; Payne and Payne 1993); 3) breeding birds disperse to find a better site (site choice; Payne and Payne 1993); and 4) breeding birds disperse as a result of social constraints (social constraints; Payne and Payne 1993).   The hypothesis that breeding birds disperse as a result of genetic predisposition (heritability; Payne and Payne 1993) is not considered in this study.

These hypotheses are not mutually exclusive; that is, more than one cause of breeding dispersal may be operating within a population or on an individual. Of special interest to me is that birds in different circumstances may disperse for different reasons. For this reason, I partition dispersal events by three broad circumstances: the death of a mate, reproductive failure, and no mate death or failure. Using these partitioned data sets, I test the following predictions of the hypotheses for the cause of breeding dispersal. Predictions are specific to the red-cockaded woodpecker; researchers cited for hypotheses may or may not have used similar predictions. All analyses are restricted to females because breeding dispersal among males of this species is very rare.

TESTS OF HYPOTHESES

Inbreeding avoidance

In this study, the hypothesis of inbreeding avoidance is applied only to females dispersing after the death of a mate. Unique to this hypothesis is the prediction that the frequency of dispersal increases when sons inherit breeding status on the female's territory (Table 2.1, prediction 1a).

Table 2.1. Predictions of four hypotheses for the cause of breeding dispersal of female red-cockaded woodpeckers.

Mate choice

The mate choice hypothesis predicts that dispersing females improve the quality of their mates, and that the frequency of dispersal increases in response to low-quality males. In this study, the measure of male quality is based on age: male reproductive success increases sharply with age until males are three years old; their success then levels off for their remaining years (Khan and Walters, in prep). Success of males ten years and older is probably reduced, but there are relatively few of these males in the population. Therefore, an appropriate measure of male quality has three values: 1, one year-old males; 2, two year-old males; and 3, males aged three years and older.

For females dispersing after the death of their mates, the mate choice hypothesis predicts that the quality of new mates on the new, receiving territories is higher than that of the males replacing dead mates on the original territories (replacement males; 2a). It also predicts that the frequency of dispersal increases if replacement males are of low quality (2b). For females dispersing while their mates survive, mate choice predicts that the quality of new mates is higher than that of the old mates (2c), and that dispersal increases if mates are of low quality (2d). These predictions are all unique to the mate choice hypothesis.

Other predictions of the mate choice hypothesis are that females whose mates survive will disperse more frequently after reproductive failure (2e) and poor reproduction (2f). These two predictions are shared by the site choice hypothesis but distinguish both mate choice and site choice from the social constraint and inbreeding avoidance hypotheses.

Site choice

Site choice predicts that the quality of new, receiving territories is higher than that of the original territories (3a), and that the frequency of dispersal decreases with the presence of helpers (3b), because helpers signify high territory quality. These two predictions are unique to this hypothesis. In addition, site choice has two predictions in common with mate choice: the frequency of dispersal should increase with reproductive failure (3c) and poor reproduction (3d).

Social constraints

Social constraints is the hypothesis that breeding birds disperse in response to intra-specific interactions (that is, dispersal is a consequence of social behavior, Payne and Payne 1993). I identified three possible interactions in the red-cockaded woodpecker: female-female competition, within-group competition for resources, and within-group reproductive competition between mothers and helper sons. Female-female competition for breeding vacancies states that females displace one another; it predicts that new females in the original sites (replacement females) are older than dispersing females (4a), because older females are dominant (J. Walters, pers. comm.). Within-group competition for resources predicts that females disperse more frequently if helpers are present on the original territory (4b), because increased group size may increase competition for resources among group members. Finally, within-group reproductive competition predicts that females disperse more frequently if helper sons are present in the group

(4c; Gowaty and Lennartz 1985). Each of these predictions are unique to the social constraint hypothesis.

ADDITIONAL ANALYSES

Age of the breeding female

The effect of various circumstances on breeding females may change with age. Therefore, I compare the ages of dispersing and site-faithful females by circumstance, and examine the relationships among age, dispersal, and reproductive failure.

Mortality by circumstance

I assess mortality by the same sets of circumstances used to examine dispersal. This analysis suggests which movements may be facultative or obligatory, because mortality can be expected to increase for those females which have no choice but to disperse. More importantly, I use mortality and dispersal rates by circumstance to estimate mortality rates for dispersers and for non-dispersers, which provides rare evidence of the cost of dispersal.

Dispersal distance

I present dispersal distances of breeding females within this population in two units: kilometers and numbers of territories crossed. I then analyze the effect of circumstance on dispersal distance to explore the possibility that distance increases as movement changes from facultative to obligatory.

METHODS

STUDY SPECIES, STUDY AREA, AND METHODS OF DATA COLLECTION

The red-cockaded woodpecker is an endangered species endemic to the pine savannas of the southeastern United States. It exhibits a system of cooperative breeding, in which roughly half of fledgling males delay dispersal and remain on the natal territories as helpers, and almost all fledgling females disperse (Walters et al. 1988). Red-cockaded woodpeckers live in groups on year-round territories, and the group can consist of a solitary male (an adult male on a territory without an adult female), a breeding pair without a helper, or a breeding pair with one or more helpers (Lennartz et al. 1987, Walters et al. 1988). Movement of females, both young and adult, is an important factor determining the number of breeding groups, and the number of breeding groups is, in turn, a critical determinant of population growth or decline in this species (Walters 1991).

The study area is located in the Sandhills of south-central North Carolina, and encompasses over 110,000 ha. Data collection began in 1980 and continues through the present. By 1982, all woodpecker groups within the study area (roughly 220) were being monitored. Individuals were banded with a unique combination of color bands and reproduction of groups

was monitored each breeding season. Most birds were banded as nestlings, and each breeding season all members of each group were identified. Therefore, placement of most individuals in the study area was determined each year. Further information concerning the study species and methods of data collection is given by Walters et al. (1988), and a detailed description of the study area is given by Carter et al. (1983).

DEFINITIONS AND MEASURES

Breeding dispersal

Breeding dispersal, for this study, is defined as movement between consecutive breeding opportunities. (Each female had one breeding opportunity per year if she was at least one year old and was the only or oldest female residing within a cluster of cavity trees: in this species, females do not occupy territories that have no male present, and do not breed in different locations in the same season). This definition of breeding dispersal includes movements between breeding sites (Greenwood 1980), movements between consecutive breeding attempts (Part and Gustafsson 1989, Montalvo and Potti 1992), and movements of adults that were in breeding positions but did not attempt to nest (i.e. do not lay eggs). The proportion of pairs that did not attempt to nest varied annually from 4 to 25 percent of all breeding pairs in this population of woodpeckers.

Reproductive failure

Reproductive failure, here, includes both failure to attempt to nest (no nest attempt) and failure to produce at least one fledgling from a clutch (nest failure). These two types of reproductive failures are combined for most analyses in order to maintain adequate sample sizes; however, the distinction between them is recognized in one set of analyses and in the Discussion.

Territory quality

I measured territory quality using both natality and mortality rates for each territory (following Ligon and Ligon 1990). A good territory produces high numbers of young and provides high survivorship for adults. I therefore divided average annual production (total fledglings produced on the territory/the number of years that territory has been monitored) by average annual adult mortality (the number of deaths of adults[1] on that territory/total number of adult bird-years):

$$TQ = \frac{(\text{TOTAL FLEDGLINGS/TERRITORY YEARS})}{(\text{TOTAL DEATHS/BIRD-YEARS})}$$

Territory quality for 327 territories ranged from 0.0 to 14.0, with a median of 2.97, a mean of 3.47, and a standard deviation of 2.62. Descriptive statistics for all components of this formula are presented in Appendix A. Territory quality was not calculated for eight territories that had no birds die there, and an additional territory for which no birds could be identified.

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[1] A bird is counted dead on a territory if it was last seen there and not seen in the following years.

Distance

Dispersal distance in kilometers is the length of the straight line between estimated territory centers. Dispersal distance in the number of territories crossed is a count of territories whose centers are within 400 meters of this straight dispersal line; the original territory was not counted but the receiving territory was, so that a bird moving next door crossed 1 territory and a bird remaining in the original territory crossed 0 territories. Only territories occupied in the year the female appears in the new location were counted.

Data collected during regular nest-monitoring and censusing activities included locations of foraging or congregating adults in universal transverse mercator (UTM) coordinates. Territory centers were estimated by the centroid of the polygon including all these location points pooled over 13 years (1980-1992). This estimation was performed by Roger Barr of N.C. State University using Atlas GIS software. For the few new territories created from 1993 to 1995, UTM coordinates of nest trees were used to estimate territory centers.

The years 1980 and 1981 were omitted from the analyses of breeding dispersal distances, because not all territories within the study site were monitored during this time. From 1982 to 1995, virtually all territories within the study site were monitored.

SAMPLE SIZES

Each female in each year either disappeared, remained in the same location, or moved to a new location. For all but one analysis, observations were pooled across years; the unit for analysis was thus female bird-years and individual females appeared more than once. There were 2698 bird-years from 16 years available for analysis. For analysis of mortality rates, all 2698 bird-years were used. For all other analyses, the following observations were deleted: 1) cases in which the breeding pair moved together (n=38) are artifacts of data collection and do not indicate true dispersal (that is, the group moved to a nearby cluster of trees that had been assigned separate territory status, but was probably a part of the original territory at that time); 2) cases in which the breeding male moved to another location (n=57) were removed because this is a rare occurrence and not the subject of this investigation; 3) cases in which the breeding male could not be identified (n=187) were deleted. Finally, sample size changed among analyses as different information was required and not all observations contained the requisite information.

STATISTICAL ANALYSES

Statistical tests varied among analyses and are identified as results are reported. All data sets were tested for normality of the underlying distributions using the Shapiro-Wilks test; if significantly different from normal (p<=0.10), non-parametric tests were used. A conservative significance level was chosen for tests of normality because normally distributed data may be appropriately analyzed with non-parametric tests, but the reverse is not correct.

RESULTS

ANNUAL FREQUENCIES OF DISPERSAL, SITE FIDELITY, AND MORTALITY

Life histories of all identified breeding females, expressed as the means of annual percentages, are presented in Figure 2.1. Each year, approximately 11 percent of breeding females dispersed to another location, 56 percent of breeding females remained site-faithful, and 31 percent of females died (some individuals included in this category may have dispersed off the study site). One percent of breeding females became floaters, which are adult birds not associated with a territory or mate and which therefore do not produce young. Walters et al. (1988) report similar rates for this population for the years 1980-1985.

die:	31%
remain:	56%
disperse:	11%
float:	1%
other:	1%
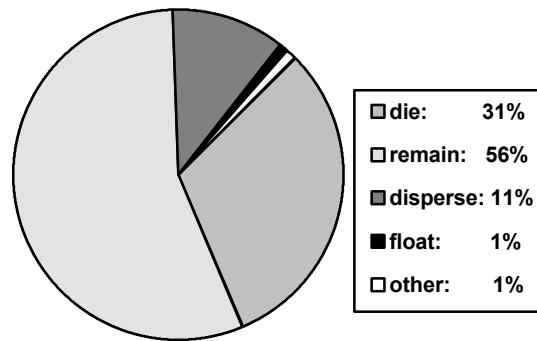
Figure 2.1. Life history of breeding female red-cockaded woodpeckers (n=2698 bird-years, mean annual percentage rates 1980-1994).

Notes: 'Other' refers to the cases in which the breeding group moved. Cases in which the male moved independently are included across categories to correctly estimate the mortality rate.

Annual variation in dispersal, site fidelity, and mortality is presented in Figure 2.2. Annual dispersal was not associated with either site fidelity or mortality, but site fidelity and mortality were highly, inversely correlated (Spearman rank; dispersal and fidelity: $r=-0.43$, $p=0.11$; dispersal and mortality: $r=-0.02$, $p=0.94$; fidelity and mortality: $r=-0.85$, $p=0.0001$). Also, annual dispersal was much less variable than were annual mortality and fidelity (Figure 2.2). Thus, breeding vacancies do not appear to drive breeding dispersal in this species, at least for the majority of dispersing females.
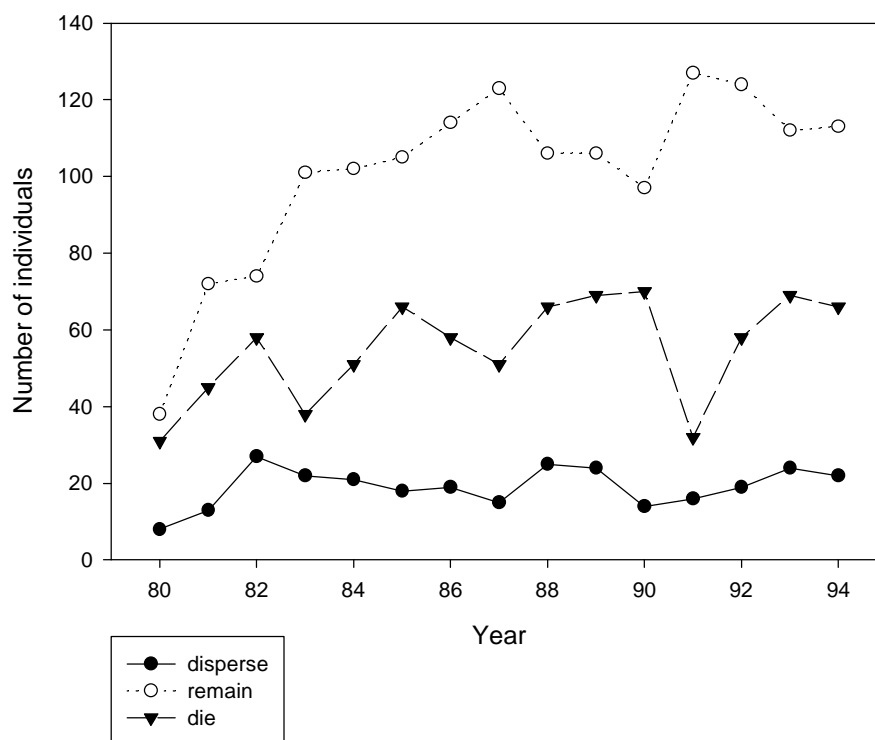
Figure 2.2. Annual variation in the number of red-cockaded woodpecker females that dispersed, remained site-faithful, or died (1980-1994). The total number of individuals increased in the early years because there were an increasing number of groups included in the census.

FREQUENCY OF DISPERSAL BY CIRCUMSTANCE

Of 242 dispersing females, 65 percent (158) moved after mate death, 38 percent (91) moved after reproductive failure, and 17 percent (42) moved after no mate death or failure. (Mate death and reproductive failure are not mutually exclusive categories; 20 percent (49) of dispersing females moved after both reproductive failure and mate death.) Reproductive failure and mate death were both significantly associated with breeding dispersal (Table 2.2).

Table 2.2. Frequencies of dispersal and site fidelity by two exclusive
circumstances: mate death only and reproductive failure only. Expected values
are given in parentheses.

Circumstance	Female dispersed	Female remained	chi-square	p-value[1]
Mate death only	109 (29)	121 (201)	313.7	0.001
No mate death or failure	42 (122)	929 (849)		
Reproductive failure only	42 (23)	317 (336)	24.1	0.001
No mate death or failure	42 (61)	929 (910)		

[1] Chi-square tests, df=1.

THE TEST FOR INBREEDING AVOIDANCE

The hypothesis of inbreeding avoidance was tested by comparing the number of times a
son attained breeding status in his mother's territory with the frequency of dispersal. There were
49 cases in which a son became the breeder, and in all but 4 of these cases the mother dispersed
(Table 2.3). The strongly significant relationship between breeding dispersal and the maternity of
the replacement male is a prediction (1a) unique to the inbreeding avoidance hypothesis and
clearly shows that the dispersal of female red-cockaded woodpeckers does serve as an inbreeding
avoidance mechanism.

Table 2.3. Frequencies of dispersal and site fidelity by maternity of the
replacement male. Expected frequencies are given in parentheses.

Maternity of replacement male	Female dispersed	Female remained	chi-square	p-value[1]
son	45 (21)	4 (28)	61.3	0.001
not a son	50 (74)	122 (98)		

[1]Chi-square test, df=1.

Because the cause of these movements is so clear, the 49 cases in which a son becomes
the breeding male were omitted from all further analyses unless their inclusion is specifically
noted. After removing these cases, mate death was still highly associated with the movement of
breeding females (chi-square test, $X^2=247$, df=1, p=0.001).

TESTS OF MATE CHOICE

Dispersal after the death of a mate

There were 282 cases in which a female's mate died, the female's son did not inherit that
territory, and the female herself either remained on territory or dispersed. In 47 of these 282
cases, no breeding male was present in the following year, and hence the site became abandoned.
In the remaining 235 cases, the vacant breeding male position was filled by a new male. The

following analyses examine the quality of these replacement males. Only males whose ages were known exactly were included.

Females whose mates died dispersed more frequently than expected if replacement males were of low quality, and remained on territory more frequently than expected if replacement males were of high quality (Table 2.4). For dispersing females, new mates on the subsequent territories were of significantly higher quality than the replacement mates on the original territories (Figure 2.3 gives population distributions; paired sign test on the difference in male quality for each female: n=47, test statistic M=14, p=0.0001). Predictions 2a and 2b, both unique to mate choice, are supported: breeding females disperse after the death of their mates to avoid young, low-quality males.
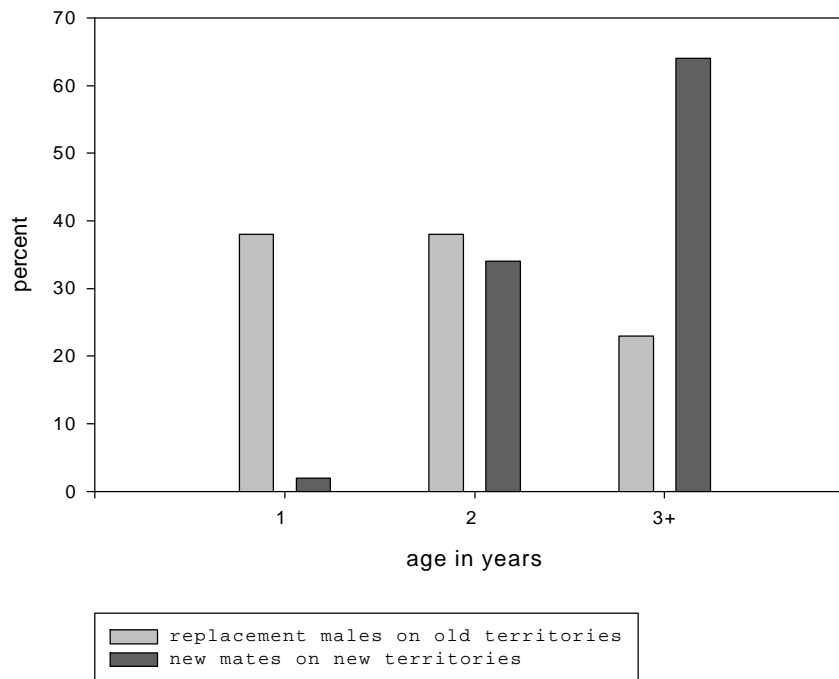
Figure 2.3. Quality of replacement males vs. new mates for females dispersing after mate death, in the year following dispersal. (N=47 dispersal events in which the exact age is known for both the replacement male and the new mate.)

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Table 2.4. Frequencies of female dispersal and fidelity after mate death, by the quality of the replacement male[1]. Expected values are in parentheses.

Female...	Quality of replacement male			X^2	p-value[2]
	1	2	3		
dispersed	25 (14)	22 (21)	12 (24)	20.8	0.001
remained	21 (32)	49 (50)	66 (54)		

[1]40 cases in which the ages of the replacement males are not known exactly are omitted from this analysis.
[2]Chi-square test, df=2.

Dispersal without the death of a mate

Females whose mates survived were more likely to disperse if their mates were young, low-quality males (Table 2.5; this analysis includes those females dispersing after reproductive failure, but excludes mates of unknown ages.) However, the quality of the original and new mates was not significantly different (Figure 2.4 gives population distributions; paired sign test on the difference in quality for each female: n=34, test statistic M=-1, p=0.73). By definition, the original mate surviving to the year following dispersal is at least 2 years old, and new mates were largely 2 years old or older (Figure 2.4). Of these two predictions unique to the mate choice hypothesis (2c,2d), only one (2c) is supported.

Table 2.5. Frequencies of female dispersal and fidelity without mate death, by the quality of the original mate[1], in the year preceding dispersal. Expected values are in parentheses.

Female...	Quality of original mate			X^2	p-value[2]
	1	2	3		
dispersed	9 (3)	11 (9)	29 (37)	13.8	0.001
remained	44 (50)	137 (139)	589 (581)		

[1]511 cases in which the ages of the original mates are not known exactly are omitted from this analysis.
[2]Chi-square test, df=2.
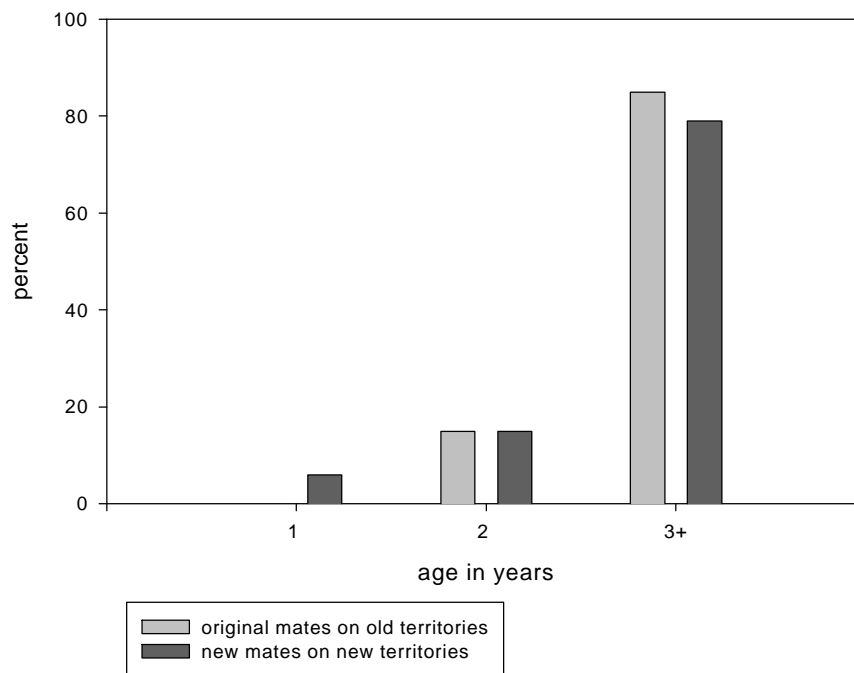
Figure 2.4. Quality of original vs. new mates for females dispersing while their mates survived, in the year following dispersal. (N=34 dispersal events in which the exact age of both original and new mates are known).

Whether the female stayed or dispersed was significantly associated with reproductive failure (see Table 2.2 above), but not with the number of fledglings produced from successful nests (Table 2.6). Of these two predictions common to both the mate choice and site choice hypotheses (2e, 2f), only one (2e) is supported. Reproductive failure was associated with the age of the male in two ways: young males failed to nest more often than older males, and young males suffered increased nest failures (Table 2.7). Frequencies of each type of failure were roughly equal for dispersing females: of 42 females dispersing after reproductive failure but no mate death, 20 suffered nest failure and 22 had not attempted to nest. Infertile males may cause nest failures, but this possible association between male quality and reproductive failure was not tested in this study.

Table 2.6. Importance of number of fledglings on the dispersal of females whose mates survived.

No. of fledglings	female disperses	female remains	X^2	p-value[1]
1	13 (10.3)	225 (227.7)	2.5	0.28
2	22 (20.5)	451 (452.5)		
3+	7 (11.5)	231 (248.8)		

[1]Chi-square test, df=2.

Table 2.7. Frequency of no nest attempt[1] and nest failure[2] by the age of the breeding male. Expected values are given in parentheses.

	Age of breeding male			X^2	p-value[3]
	1	2	3+		
Attempts	67 (94)	205 (211)	964 (931)	66.4	0.001
No attempts	41 (14)	39 (33)	111 (144)		
Nest failed	26 (12)	49 (36)	140 (168)	33.0	0.001
Nest did not fail	41 (55)	156 (169)	824 (796)		

[1] n=1427 events in which the exact ages of males are known.
[2] n=1236 events in which the exact ages of males are known and nests were attempted.
[3] Chi-square test, df=2.

TESTS OF SITE CHOICE

Territory quality, as measured by my quality index (see Methods), was not significantly different between new and old territories for those females dispersing after mate death (paired t-test on the difference between territories: n=108, test statistic T=-1.45, p=0.59), nor for those females dispersing after reproductive failure only (n=42, T=-0.69, p=0.49), nor for those females dispersing after no mate death or reproductive failure (n=42, T=0.67, p=0.51). Prediction 3a, unique to this hypothesis, is not supported.

The presence of helpers on the original territory, a sign of high territory quality, did not affect dispersal of females whose mates died (excluding sons inheriting, chi-square test, n=282, df=1, X^2=1.7, p=0.19). However, the presence of helpers significantly decreased the dispersal of females whose mates survived (Table 2.8). Helpers may reduce the probability of nest failure, but their negative association with female dispersal remained significant even when the effect of reproductive failure was controlled (categorical model using maximum likelihood estimates: presence of helpers=-0.65, X^2=12.95, p=0.0003; reproductive failure=0.46, X^2=16.03, p=0.0001; chi-square test excluding reproductive failures, Table 2.8). Thus, prediction 3b is supported for those females whose mates survive, but not for those whose mates died.

Table 2.8. Importance of helpers on the dispersal of females whose mates survived, with and without reproductive failure.

Circumstances	female disperses	female remains	X^2	p-value[1]
Mate remains-				
helpers present	9 (27.3)	423 (404.7)	19.4	0.001
helpers absent	75 (56.7)	823 (841.3)		
Mate remains,				
reproductive failures omitted-				
helpers present	5 (15.6)	355 (344.4)	11.9	0.001
helpers absent	37 (26.4)	574 (584.6)		

[1]Chi-square tests, df=1.

Reproductive failure, regardless of mate death, was significantly associated with dispersal (prediction 3c is supported; see Table 2.2 above), which supports this hypothesis to the extent that site quality contributes to such failures. Low numbers of fledglings from successful nests did not appear to influence whether a female disperses (prediction 3d is not supported; see Table 2.6 above).

TESTS OF SOCIAL CONSTRAINTS

Female-female competition

The test for female-female competition is a comparison of the ages of dispersing females and those of the females replacing them. However, roughly 40 percent (64 of 158, including sons inheriting) of females dispersing after mate death were not replaced; of these 64 cases, 34 sites became abandoned and 30 sites contained a new, solitary, male. One fifth (17 of 84) of females dispersing while their mates survived were not replaced; their former mates became solitary males.

In 65 dispersal events in which the ages of both the replacement female and the dispersing female were known exactly, replacement females were significantly younger than dispersing females by an average of 1.4 years and a median of 1 year (paired sign test on the age difference between each set of females, n=65, test statistic M=23, p=0.0001; see Figure 2.5 for population distributions). Of these 65 dispersal events, replacement females were older than dispersing females in only 7 cases. Replacement females were younger than dispersing females in 53 cases, and equal in age in 5 cases. Of the 7 instances in which replacement females were older than dispersing females, 3 included the death of the mate, 2 included reproductive failure, and 2 occurred after no mate death or failure. Thus, prediction 4a is not supported.
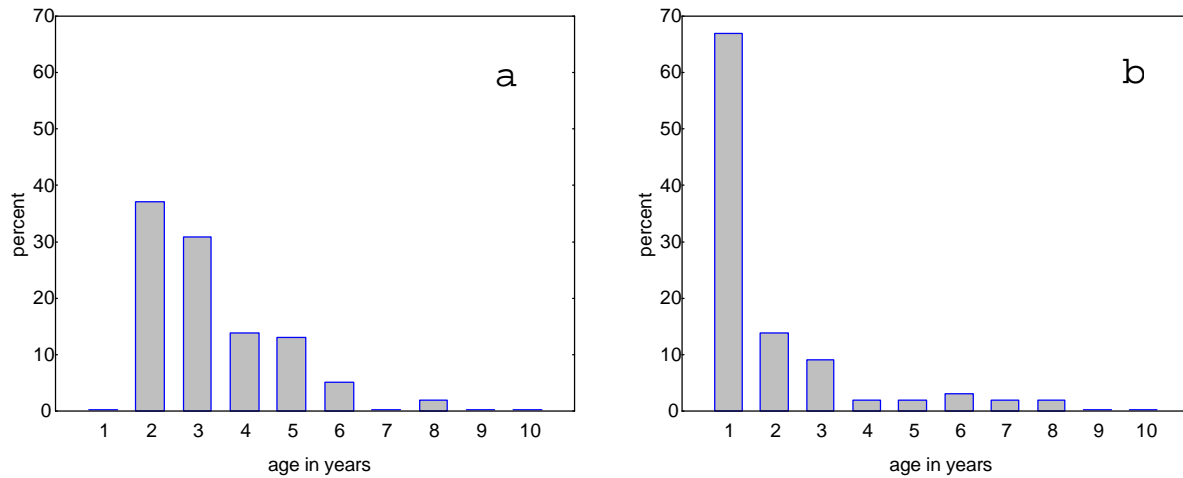
Figure 2.5. Ages of dispersing (a) and replacement (b) females for 65 dispersal events in which exact ages of both females were known.

Within-group competition for resources

Although the presence of helpers may increase within-group competition, it was not associated with breeding dispersal after mate death and was negatively associated with dispersal while the mate remains on territory (see Table 2.8 above). Prediction 4b is not supported; there is no evidence that within-group competition influences breeding dispersal.

Within-group reproductive competition

Reproductive competition predicts that females will disperse more often if helper sons are present on the original territory (4c); however, this did not appear to be true for red-cockaded woodpeckers. To exclude the effect of sons inheriting, I only considered cases in which the breeding male survived, and helpers were present. Females dispersed only 5 times in the presence of helper sons; they remained on territory in the presence of helper sons 233 times (Table 2.9). These numbers are too low for statistical analysis, but the very fact that dispersal was so low when helpers were present is evidence against this hypothesis.

Table 2.9. Importance of helper sons on the dispersal of females whose mates survived.

Circumstances	Female disperses[1]	Female remains
1 or more unrelated helpers present	3	162
1 or more helper sons present	5	233

[1]In one case of dispersal maternity of the helper was unknown.

AGE OF THE BREEDING FEMALE

Dispersing females were significantly younger than site-faithful females for all circumstances combined (Figure 2.6a; median one-way analysis, X^2=9.3, df=1, p=0.002). For females experiencing mate death, those dispersing were equal in age to those remaining (Figure 2.6b; X^2=1.5, df=1, p=0.22); for females experiencing reproductive failure, those dispersing were significantly younger than those remaining (Figure 2.6c; X^2=8.2, df=1, p=0.004); and for females experiencing neither mate death or failure, those dispersing were also significantly younger than those remaining, although sample size for this last category was low (Figure 2.6d; X^2=6.1, df=1, p=0.01).

Among the dispersing females, females moving after reproductive failure were significantly younger than females moving after the death of their mates and females moving after no mate death or failure (Table 2.10; median one-way analysis, X^2=11.5, df=2, p=0.003). Young, inexperienced females were more susceptible to reproductive failure, however: the frequencies of both nest failure and no nest attempt were higher than expected for one year-old females (Table 2.11).

Table 2.10. Ages of dispersing females by circumstance.

Circumstance	mean age	median age	n
reproductive failure only	1.44	1	32
mate death only	2.64	2	42
no mate death or reproductive failure	2.24	2	21

Table 2.11. Frequency of no nest attempt[1] and nest failure[2] by the age of the breeding female. Expected values are given in parentheses, below actual frequencies.

| | Age of breeding female | | | | | | |
	1	2	3	4	5+[3]	X^2	p-value[4]
Attempt	355	348	255	169	231	121.6	0.001
	(422)	(338)	(236)	(153)	(210)		
No attempt	132	42	17	8	11		
	(65)	(52)	(36)	(24)	(32)		
Nest failed	98	69	38	19	34	29.3	0.001
	(67)	(66)	(48)	(32)	(44)		
Nest did	257	279	217	150	197		
not fail	(288)	(282)	(207)	(137)	(187)		

[1] n=1568 cases in which females' exact ages are known.
[2] n=1358 cases in which females' exact ages are known, no attempts omitted.
[3] Birds aged 5 and above are grouped to maintain cell sample size.
[4] Chi-square test, df=4.
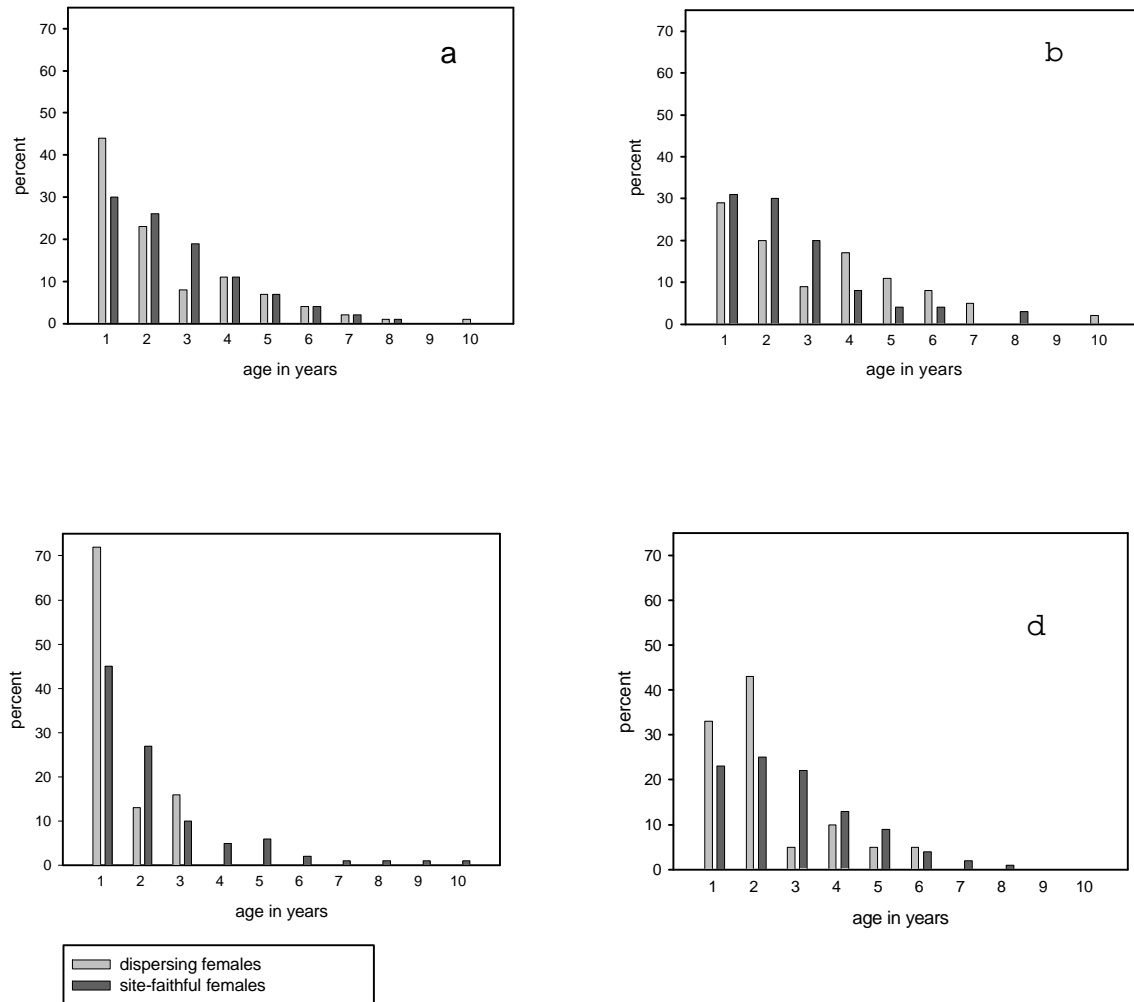
Figure 2.6. Age distributions of dispersing and site-faithful females for the following circumstances: a) all females (n=153, 939); b) mate death only (n=65, 74); c)reproductive failure only (n=32, 213); and d) no mate death or reproductive failure (n=21, 614). Only females whose exact ages are known are included.

To reveal whether the effect of age on reproductive failure depends entirely on the behavior of one year-olds, I repeated the analyses presented in Table 2.11 with one year-olds excluded. Age was still significantly associated with no nest attempt (X^2=12.2, df=3, p=0.007) and marginally associated with nest failure (X^2=7.5, df=3, p=0.057). After excluding both one and two year-old females from analysis, age was not significantly associated with either no nest attempt (X^2=0.98, df=2, p=0.63) or nest failure (X^2=1.5, df=2, p=0.45). Some two year-old females did not obtain breeding vacancies as one year-olds, and so it is likely that the effect of age on reproduction reflects reduced success for novice breeders.

To detect whether reproductive failure promotes dispersal among older females, I repeated the analysis presented in Table 2.6, but excluded all females not known to be at least two years-old. Reproductive failure (without mate death) was still significantly associated with dispersal when one year-olds were excluded ($X^2=6.1$, df=1, p=0.013). Sample sizes were too low to perform a similar analysis with both one and two year-olds excluded. When, however, the instances of both reproductive failure and mate death were included, reproductive failure was not significantly associated with dispersal for females three years old and older ($X^2=2.2$, df=1, p=0.15). Therefore, the dispersal of young females is increased by reproductive failure; the dispersal of older females (>2 years) is unaffected by reproductive failure.

DISTANCE DISPERSED BY BREEDING FEMALES

249 movements were available for these analyses. Distributions of dispersal distances are presented in Figure 2.7. The two measures, distance in kilometers and distance in numbers of territories crossed, were correlated (Spearman rank, R=0.68, p=0.0001). Presumably, any difference between the two measures reflects territory density.

Dispersal distances for breeding females were generally very short, and more than half moved to a neighboring territory (Figure 2.7). Dispersing females moved a median of 1 territory or 1.3 kilometers, and a mean of 1.8 territories or 2.1 kilometers from their original breeding site (Figure 2.7).
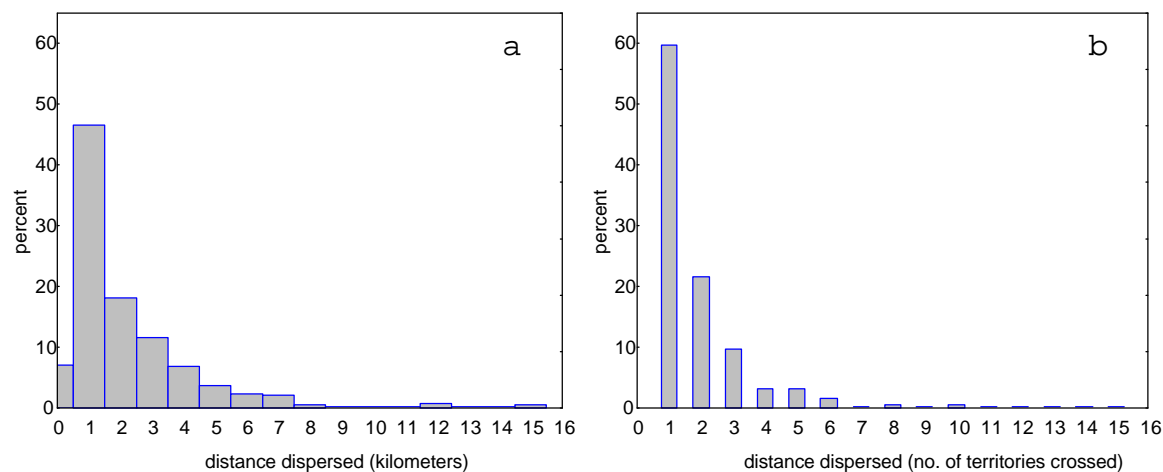
Figure 2.7. Distance that breeding females disperse (n=249), in two units: a) kilometers (continuous), and b) number of territories crossed (discrete).
Notes on sample sizes:
1. Unknown males (n=20) are included.
2. Sons inheriting are included.
3. 13 dispersal events occurring before 1982 are omitted.

Dispersal distance by circumstance

Table 2.12 presents two measures of dispersal distance by the circumstances of dispersal. Here, the cases where sons inherit territories were included in the analysis. Birds dispersing after neither mate death or reproductive failure moved significantly shorter distances than birds dispersing after mate death or reproductive failure (median tests; a) km: death only vs. no death or failure, n=104,39, X^2=12.3, df=1, p=0.0005; death only vs. reproductive failure only, n=104,41, X^2=2.9, p=0.09; no death or failure vs. reproductive failure only, n=39, 41, X^2=17.8, p=0.0001; b) no. territories: death only vs. no death or failure, X^2=4.9, df=1, p=0.03; death only vs. reproductive failure only, X^2=1.3, df=1, p=0.26; no death or failure vs. reproductive failure only, X^2=7.8, p=0.005). Birds dispersing after no mate death or reproductive failure may opportunistically occupy neighboring vacancies rather than dispersing to avoid a fitness-threatening situation on the original territory. Dispersal for these females appears to be facultative.

If obligate dispersal entails longer dispersal distance, then birds dispersing when their sons inherit the natal territories would be expected to move the furthest distance. As a group these birds did move the furthest, but the difference in dispersal distance between those moving after their sons inherited and those moving after an unrelated male acquired the territory was not significant (Table 2.13).

Table 2.12. Dispersal distance (km. and no. territories) by circumstance.

Unit	Circumstance	mean	median	max	min	N
kilometers:	reproductive failure only	2.4	2.1	11.7	0.5	41
	mate death only	2.3	1.5	12.4	0.03	104
	no mate death or reproductive failure	1.5	0.8	14.8	0.5	39
no. of territories:	reproductive failure only	2.0	2	8	1	41
	mate death only	1.8	1	6	1	104
	no mate death or reproductive failure	1.5	1	10	1	39

Table 2.13. Dispersal distances (km and no. territories) of females moving after mate death by maternity of the new breeding male.

Unit	maternity	mean	median	max	min	N	X^2	p-value[1]
kilometers:	son	2.7	2.0	8.0	0.5	44	0.7	0.41
	not a son	2.0	1.4	7.2	0.4	59		
no. of territories:	son	2.1	2	6	1	44	2.5	0.10
	not a son	1.7	1	5	1	59		

[1] median test, df=1.

MORTALITY RATES BY CIRCUMSTANCE AND THE COST OF DISPERSAL

Across circumstances, mortality rates increased with increasing rates of dispersal (Table 2.14); this correlation was significant (Spearman rank, $R=0.9$, $p=0.037$). Under certain circumstances, such as the son inheriting, almost all females disperse, and mortality is high. Under other circumstances, such as no mate death or reproductive failure, few females disperse, and mortality is low. This information can be used to estimate both the cost of dispersal and the mortality rate for females that do not move (background mortality). Figure 2.8 presents a plot of mortality for all females and dispersal rates of survivors by circumstance. The y-intercept on the left (0 percent dispersers) is the estimate of background mortality: an estimated 24 percent of breeding females that did not disperse died each year. Average annual mortality rate for all breeding females was 31 percent (Figure 2.1), and so breeding dispersal was the source of annual mortality for 7 percent of breeding females in this population. Mortality of dispersers is estimated by the y-intercept on the right (100 percent dispersal of survivors). For an unidentified circumstance in which all females attempt to disperse, 59 percent of females die. If the mortality rate of dispersing females is constant across circumstances, an estimated 59 percent of females that attempt to disperse die.

$$y=0.33x + 25.87$$
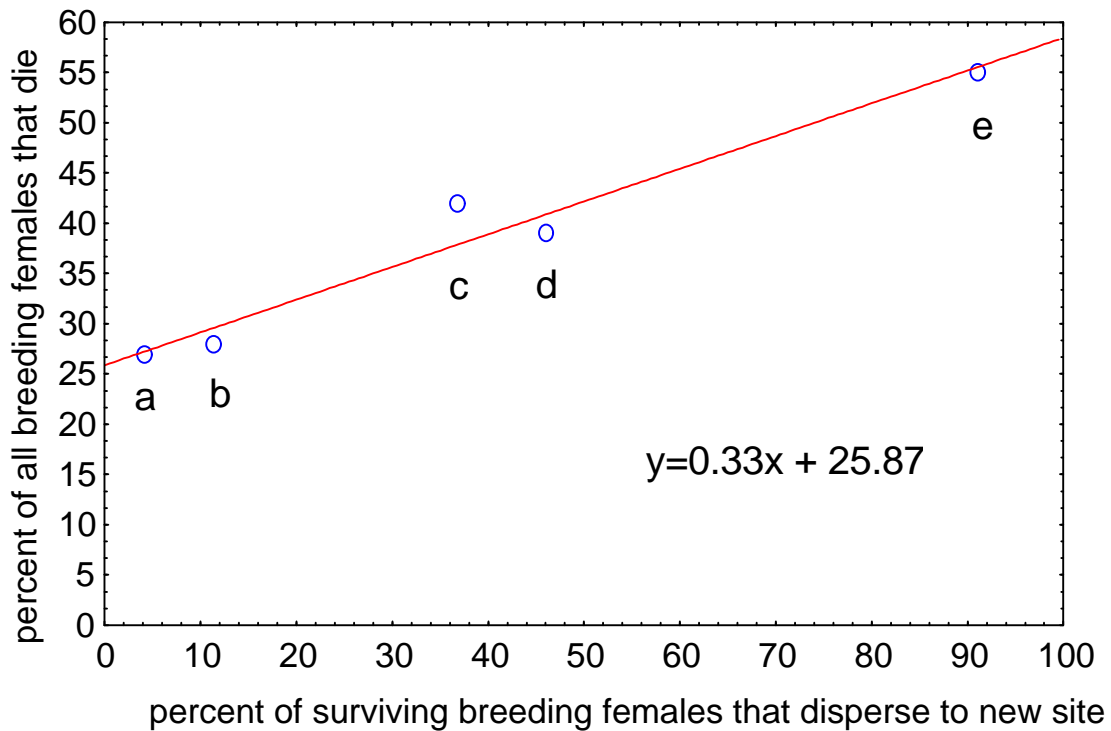
Figure 2.8. Rates of breeding dispersal within circumstance, in percent of all females in that circumstance, plotted against mortality (disappearance) rates for the same groups of females. Circumstances are exclusive categories, as follows: a: no mate death or reproductive failure, n=1327; b: reproductive failure, n=501; c: mate death and reproductive failure, n=159; d: mate death, n=321; e: son inherits, n=108.

Table 2.14. Fate by circumstance.

Circumstance	% disappear	% disperse	% remain
Son inherits (n=108)	55	41	4
Death of mate only[1] (n=321)	42	21	36
Reproductive failure and mate death[1] (n=159)	39	28	33
Reproductive failure only (n=501)	28	8	63
No mate death or reproductive failure (n=1327)	27	3	70

[1]Cases in which the son inherits are omitted from these categories.

Dispersal distances by circumstance (see Tables 2.12 and 2.13 above) were ordered in almost the same way as mortality and dispersal rates (Table 2.14), which suggests that obligatory dispersal may result in longer dispersal distances. This remains merely a suggestion, however, because the differences among dispersal distances were not significant except for the short movements of those dispersing after no mate death or reproductive failure.

DISCUSSION

Meaningful results of this study are a) evidence of multiple causes of breeding dispersal within a population, including clear documentation of inbreeding avoidance and mate choice and some support for site choice; b) elimination of social constraints as a cause of breeding dispersal in this species; c) clarification of the relationships among reproductive failure, age, and breeding dispersal; and d) important estimates of mortality rates for females that disperse and for those that remain on territory, two population parameters that have been notoriously difficult to identify.

MULTIPLE CAUSES OF BREEDING DISPERSAL

This study clearly shows multiple causes of breeding dispersal within a population of red-cockaded woodpeckers. Much of the previous research into breeding dispersal has lent support to one hypothesis of causation to the exclusion of others, without explicitly recognizing the possibility of multiple causes. Certainly an approach using partitioned data sets based on the circumstances of dispersal and fidelity, recognizing factors such as sex, age, and those used in this study (e.g. mate death, reproductive failure, no mate death or reproductive failure), is more likely to reveal multiple causes of breeding dispersal than the approach of using one unpartitioned data set. A few studies support multiple causes of breeding dispersal. Payne and Payne (1993) report more than one cause of breeding dispersal in indigo buntings (*Passerina cyanea*): females disperse to find a better site, and males disperse because of social constraints. Walters et al. (1988) also suggest multiple causes of breeding dispersal in red-cockaded woodpeckers: inbreeding avoidance is shown convincingly, site choice is supported although weakly, and both mate choice and social constraints are suggested.

This study presents strong support for the hypotheses that breeding female red-cockaded woodpeckers disperse to avoid inbreeding and to attain a higher quality mate: predictions unique

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to each of these hypotheses are validated. This study presents weak support for the hypothesis that breeding females disperse to attain a higher quality territory: one unique and one shared prediction are validated. There is no evidence in support of the hypothesis that females disperse because of social constraints: no predictions were validated. Discussions of the implications of these hypotheses tests are presented below.

INBREEDING AVOIDANCE

Inbreeding avoidance is a common cause of breeding dispersal among cooperatively breeding birds (Walters et al. 1988). Close inbreeding (f>=0.25) is avoided in the acorn woodpecker (*Melanerpes formicivorus*; Koenig and Pitelka 1979), Florida scrub jay (*Aphelocoma coerulescens*; Woolfenden and Fitzpatrick 1984), and red-cockaded woodpecker (Walters et al. 1988). Walters et al. (1988), studying this population of red-cockaded woodpeckers in the years 1980-1985, report movement of the breeding female in 14 of 15 cases in which a son attained breeding status in the female's territory. Here, I report movement in 45 of 49 such cases in the years 1980-1995. Close inbreeding results in a loss of fitness in this species (Chapter 3); the combination of inbreeding depression and the frequency of inbreeding avoidance clearly demonstrates that breeding dispersal under these circumstances is an adaptive behavior.

Proximate mechanisms for inbreeding avoidance remain untested in this species. Kin recognition may be based on familiarity; that is, birds may assign kinship to residents of the same nest or territory (Walters 1990). If in place, this mechanism must be more sophisticated than it may at first appear. Of the cases in which a helper that was not the female's son but was present on that territory for at least a year inherited the breeding male position, the female stayed 48 times and dispersed only 5 times.

MATE CHOICE

Improvement in mate quality (mate choice) is an important cause of breeding dispersal in many species of birds, including the black-capped chickadee (*Parus atricapillus*; Otter and Ratcliffe 1996), the blue tit (*Parus caeruleus*; Dhondt and Adriaensen 1994), and Darwin's finch (*Geospiza conirostris*; Grant and Grant 1987). Mate choice is often more important in the dispersal of breeding females than males; it is usually illustrated by females switching to older males (Dhondt and Adriaensen 1994, Grant and Grant 1987) but sometimes by females switching to more dominant males (Otter and Ratcliffe 1996). Here, mate choice is manifested by females moving to avoid young males, especially after their mates have died.

In this study, the influence of the age of replacement males on dispersal of breeding females is revealed in two ways: 1) females disperse more frequently if replacement males are young, and 2) for dispersing females, replacement males on the original territories are significantly younger than the new mates on the receiving territories. Reproductive failure-- both no nest attempts and nest failure-- is strongly associated with the age of the breeding male. While the causes of reduced success have not been documented, inexperienced males do exhibit substantial difficulty reproducing. Thus, the loss of fitness that would occur through mating with

a young male combined with the higher frequency of movement away from young males clearly shows that breeding dispersal under these circumstances is an adaptive behavior.

There is no clear evidence that female red-cockaded woodpeckers disperse to improve male quality if their mates survive. Females disperse more frequently if their mates are young, and young females disperse more frequently after reproductive failure. However, females dispersing while their mates survive do not acquire older mates. In addition, there is no evidence that low productivity of successful nests prompts dispersal.

If females dispersing after reproductive failure had remained on territory, the chances of another failure would presumably be reduced as their mates age. Therefore, the associations among male age, reproductive failure, and dispersal of young females are not clear evidence for the mate choice hypothesis.

By definition, males that survive but are left by females are at least two years old, while no such constraint exists for the replacement males discussed above. It may be that, in the set of males two years of age and older, there is not enough variation in male quality to promote the dispersal of breeding females. Alternatively, perhaps females disperse from surviving mates to improve male quality, but this quality is not reflected by male age.

Proximate mechanisms to judge male quality are unknown. In the cases of mate death, the age of immigrant replacement males strongly affects the decision to move. Females may be able to discern the age of strange males by behavior or appearance, or instead may leave if no immediate replacement arrives-- a sign that the incoming male may be a dispersing yearling, rather than a nearby helper. Indications of male quality other than age undoubtedly exist, but remain unknown even in this well-studied species.

Male quality is difficult to separate from territory quality with respect to both proximate mechanisms and ultimate significance. A female may judge a male by the quality of the site he defends rather than something intrinsic to the male himself; in this scenario, it is the male that provides higher fitness and the territory is an indicator of that choice. This may be equally possible in the reverse: a female may judge a territory by the quality of the male present, but the territory produces the fitness effect (see below). Finally, there could well be site-male interactions, where a high-quality male and a high-quality territory together provide the female with higher fitness than the contribution of each one separately.

SITE CHOICE

Relatively few studies of breeding dispersal have shown that birds disperse to obtain a better site, in part because of the difficulty in separating site and mate quality, but also because many studies of mate change (i.e., dispersal without the death of a mate) have focused on mate effects rather than site effects (reviewed by Choudhury 1995). However, site choice clearly causes breeding dispersal in the following species: Tengmalm's owls (*Aegolius funereus*), which move after depletion of site resources (Korpimaki 1993), female indigo buntings, which change sites more often after unsuccessful nests regardless of the fate of their mates (Payne and Payne

1993), and pied flycatchers (*Ficedula hypoleuca*), which move to higher quality nestboxes as they age (Montalvo and Potti 1992).

Nest failure and low reproduction from successful nests are important to breeding dispersal at both the ultimate and proximate levels. Both could be indicators of low quality territories and as such serve as proximate mechanisms, and both suggest that birds disperse to increase fitness, the ultimate cause of adaptive behavior. Nest failure and/or low reproduction from successful nests have been shown to be associated with breeding dispersal in many species of birds, including red-winged blackbirds (*Agelaius phoeniceus*; Beletsky and Orians 1991), kittiwakes (Coulson and Thomas 1983), great tits (*Parus major*; Harvey et al. 1979, Linden 1991), eastern kingbirds (*Tyrannus tyrannus*; Murphy 1996), pied flycatchers (Montalvo and Potti 1992), collared flycatchers (*Ficedula albicollis*; Part and Gustafsson 1989), and bobolinks (*Dolichonyx oryzivorous*; Gavin and Bollinger 1988). Nest failure prompts within-season breeding dispersal in prairie warblers (*Dendroica discolor*) and other passerines, probably illustrating predator avoidance (Jackson et al. 1989). Nest failure and/or low reproduction from successful nests is not associated with breeding dispersal in blue tits (Dhondt and Adriaensen 1991) or willow tits (*Parus montanus*; Orell et al. 1994).

This study reveals mixed evidence for site choice as a cause of the dispersal of female red-cockaded woodpeckers. Two predictions of this hypothesis are validated: dispersal decreases with the presence of helpers, which are known to enhance reproduction (Walters 1990), and dispersal increases with reproductive failure among young females.

For dispersing females, reproductive failure is equally divided into nest failure and no nest attempt. Nest failure may be considered an effect of site quality if it is caused by predation or inter-specific competition for cavities. In either case, young males and females may be more susceptible to nest failure if proper nest defense is a skill learned through experience. Nest predation is considered relatively rare in this species because of the sap barrier created by the birds; nest failure caused by competition for cavities is considered more common (Walters 1990). In general, however, the causes of nest failure are not well documented. No nest attempt may conceivably be due to low site quality, and the high annual variability in the number of groups not nesting suggests that the environment has some influence on this behavior. Yet, this supposition leaves no explanation for the association between breeder age and failure to nest, because dispersal among breeding males is extremely rare.

Other predictions of the site choice hypothesis are not validated: I find no evidence that dispersal is influenced by low reproduction from successful nests, and no evidence that dispersal increases territory quality as measured by my index (annual production of fledglings divided by annual adult mortality).

Certainly the site choice hypothesis cannot be ruled out because the site quality index used here failed to increase upon dispersal. This index is calculated from reproduction and mortality in all the years a territory existed during the study period. Its use assumes that females are able to discern something about a territory which reflects past and future demographics over this same period; in short, it assumes that territory quality is highly stable. Yet, a similar index based on a

shorter time period would not separate male-quality from site-quality effects on reproduction, and would include greater sampling error in estimated mortality. For this species, an estimate of territory quality possibly distinct from male quality may be the number of good cavities each territory contains (Davenport 1994). These data are not presently available for analysis.

SOCIAL CONSTRAINTS

Breeding dispersal caused by social constraint has rarely been shown in birds, perhaps because this hypothesis is lacking in the conceptual framework used by the many researchers of mate change (reviewed by Choudhury 1995). It is implicitly shown in an experimental study of mate change in black-capped chickadees (Otter and Ratcliffe 1996), in which 13 females with high-quality mates were removed from the population. Dispersing females filling these vacancies consistently acquired mates of higher quality than their previous mates; thus, mate choice is supported. Upon reintroduction, the removed females displaced the new females in all cases but one. While this female-female competition is noted by the authors it is not explicitly discussed as a possible cause of dispersal in an unmanipulated population. Social constraint is explicitly shown to cause breeding dispersal in male indigo buntings (Payne and Payne 1993): older, presumably dominant males are much less likely to disperse than young males.

There is no evidence that social constraint causes dispersal of adult female red-cockaded woodpeckers. Within-group competition and reproductive competition are not supported as causes of breeding dispersal in this species because the number of helpers is negatively rather than positively associated with dispersal rates, and dispersal from territories containing helper sons is rare in the absence of mate death.

Female-female competition for breeding vacancies probably occurs among female red-cockaded woodpeckers, but there is no evidence that this competition drives breeding dispersal. Replacement females are younger than dispersing females both as a group and in 58 of 65 dispersal events in which both ages are known exactly. Five of the 7 dispersal events in which replacement females are older than dispersing females include other circumstances shown to cause breeding dispersal (mate death and reproductive failure). Replacement females may be dominant to dispersing females only if dominance is not associated with age.

Dominance could be governed by size, weight, or behavior, rather than age. Further research is necessary before intra-sexual competition is completely ruled out as a cause of breeding dispersal, but it is surprising that no influence of age-based dominance was found.

Aggressive female-female interactions are observed every breeding season in this population of red-cockaded woodpeckers, and it has long been assumed that resident breeding females are at times displaced by immigrant females. In light of results presented here, I give three possible interpretations of these aggressive interactions: 1) the females are not contesting the breeding position but, rather, group affiliation for the immigrant female, 2) immigrant females are testing to see if there is a breeding female present, or 3) the resident wins.

A final explanation for the lack of evidence of age-based dominance influencing breeding dispersal is that no competition for breeding positions exists among breeding females. Breeding females may simply be filling vacancies that have been created through the substantial mortality rate of breeding females. Older females may be dominant to first-year females, and competition for breeding positions may exist only among first-year females.

AGE OF THE BREEDING FEMALE

Young female red-cockaded woodpeckers are more likely to disperse than older birds, in large part because of the associations among reproductive failure, female age, and breeding dispersal. Both the likelihood of reproductive failure and the frequency of dispersal in response to reproductive failure are increased for females two years of age and younger. Inexperienced females are more likely to suffer nest failure and less likely to attempt to nest than older females, but the behavioral and/or physiological causes of these effects remain obscure. The interaction of reproductive failure and female age on dispersal has also been documented in the collared flycatcher (Part and Gustafsson 1989). Part and Gustafsson (1989) propose that the amount and quality of prior local experience inversely affect both the frequency of dispersal and dispersal distance; this could well be true for the red-cockaded woodpecker.

MORTALITY RATES

Mortality rates of breeding females increase under certain circumstances just as dispersal rates increase under these same circumstances. Most notably, mortality and dispersal rates reach 55 and 41 percent respectively for those females whose sons inherit breeding status on her territory. Dispersal under this circumstance appears to be both obligatory and costly.

Plotting mortality and dispersal rates within circumstance allows partitioning of mortality rates into those for dispersers and for non-dispersers. An estimated 59 percent of dispersing female breeders die, whereas an estimated 24 percent of non-dispersing female breeders die. Breeding dispersal causes an additional 7 percent mortality for all breeding females in the population. These figures may be the first estimates of the cost of breeding dispersal among birds.

While dispersal and mortality rates covary with circumstance, annual variation in these rates is not correlated (Figure 2.2). This suggests that dispersal of breeding females is generally not affected by the number of vacancies available in the population, but rather by events occurring on the original territory that are independent of female mortality.

DISPERSAL DISTANCE

Relatively few studies report distances for breeding dispersal (Table 2.15), and almost none report distances measured in actual number of territories crossed (but see Grant and Grant 1987). Distance in kilometers is strongly affected by territory size and density; distance measured in numbers of territories crossed is more informative and better for comparisons across species (Greenwood and Harvey 1982).

Table 2.15. Breeding dispersal distances (km.) for some species of birds.

Species	Distance, males	Distance, females	Source
Indigo bunting	0.6 (mean)	0.4 (mean)	Payne and Payne (1993)[1]
pied flycatchers	0.05-0.1 (median)	0.1-0.15 (median)	Part and Gustafsson (1989)[2]
Collared flycatchers	0.1 (median)	0.15 (median)	Montalvo and Potti (1992)
Red-cockaded woodpeckers		1.3 (median) 2.1 (mean)	Walters et al. (1988); this study

[1] Averaged from Table 7.
[2] Range given in Figure 2.

Dispersal distances for breeding red-cockaded woodpeckers are generally very short: more than half disperse to the neighboring territory (Figure 2.6). Despite these short distances, dispersal behavior still has important implications for population genetics. First, the clear inbreeding avoidance behavior lowers the incidence of closely related pairs. Second, although long-distance dispersal is rare among breeding females, there are a few that travel six, eight, or ten territories away. In light of the short distances for natal dispersal in this species (Chapter 4), such relatively long dispersal distances by even a few breeding females may provide substantial gene flow.

There appears to be a relationship between the circumstances of dispersal and dispersal distance, but conclusive evidence is lacking. Dispersal distances follow the same general order among circumstances as do dispersal frequencies, which suggests that obligatory dispersal results in longer distances. Birds that disperse for no apparent reason, i.e. after no mate death or reproductive failure, disperse significantly shorter distances than birds in other circumstances, but this was the only significant relationship found. While the independence of annual mortality and dispersal rates suggests that most females do not disperse in response to vacancies, it is possible that a small proportion of breeding females move to a neighboring territory because a vacancy arises. What benefit, if any, these females obtain remains unclear.

CONCLUDING REMARKS

Breeding female red-cockaded woodpeckers disperse to avoid fitness-threatening situations such as young mates, related mates, and probably some causes of nest failure. Most of these females occupy a nearby territory with a vacancy for a breeding female; dispersing females do not displace resident breeders. Some females move to neighboring vacancies without facing fitness-threatening circumstances, but the cause(s) and adaptive value of this behavior remains unclear. Breeding dispersal adds an estimated 7 percentage points to the annual mortality rate for breeding females. Further research, even for this well-studied species, is necessary to determine: a) proximate means of avoiding young and related mates, b) a better estimate of site quality and its effects on breeding dispersal, c) the heritability of breeding dispersal, d) the causes of reproductive failure and its interaction with breeder age, and e) why some breeding females may choose to disperse without facing any identified threat to fitness.

CHAPTER 3: THE COSTS, BENEFITS, AND FREQUENCY OF INBREEDING

INTRODUCTION

Inbreeding is a complex and controversial subject with important implications for the evolution and conservation of wild populations. In this study I assess the costs, benefits, and frequency of inbreeding within a population of red-cockaded woodpeckers.

INBREEDING

Inbreeding is, simply, mating between related individuals; related individuals share alleles that are identical by descent from a common ancestor (Crow and Kimura 1970). Because all animals have a common ancestor, kinship is defined relative to a specified reference: the population or the species (Wright 1978). Inbreeding has one necessary consequence: increased homozygosity. The effects of increased homozygosity may vary across time, and among species, populations, and individuals (Templeton and Read 1983, Brewer et al. 1990, Miller 1994).

COSTS OF INBREEDING

Inbreeding depression is the reduction in fitness that occurs in some species when related individuals mate. This reduction in fitness has two genetic sources: increased expression of lethal, semi-lethal, and slightly deleterious recessives, and loss of overdominance fitness effects (Wright 1977). Loss of overdominance may play a minor role compared to that of deleterious recessives (Charlesworth and Charlesworth 1987). Lethal and semi-lethal recessive alleles may be purged from a population through inbreeding and selection (Templeton and Read 1983; Falconer 1989), although slightly detrimental alleles may become fixed rather than purged through this process (Charlesworth and Charlesworth 1987; Hedrick 1994).

Inbreeding depression most often occurs in species that are adapted to large outcrossing populations (Lande 1988). It is well documented in captive populations of animals (Ralls et al. 1979, Ralls and Ballou 1983), in experimental populations of *Drosophila* (Simmons and Crow 1977) and *Peromyscus* (Brewer et al. 1990, Keane 1990), and in domestic poultry (Schoffner 1948, reviewed in Woodard et al. 1982). Close inbreeding without selection in domestic poultry reduces hatching rates and egg production (Schoffner 1948, Flock et al. 1991). Egg production and hatching rates were significantly depressed in red-legged partridge after one generation of full-sib mating (Woodard et al. 1982). Most evidence of inbreeding depression is from captive animals, but there is growing evidence that the costs of inbreeding are increased under natural conditions (reviewed by Pusey and Wolf 1996, see also Miller 1994).

Evidence of inbreeding depression in wild birds is slowly accumulating. Survival of song sparrows (*Melospiza melodia*) through severe weather is clearly reduced by inbreeding (Keller et al. 1994). In great tits (*Parus major*), closely related pairs and inbred individuals experience reduced hatching rates (Bulmer 1973; Greenwood et al. 1978, van Noordwijk and Scharloo 1981)

but no reduction in the number of young recruited into the breeding population (van Noordwijk and Scharloo 1981). Reduced hatching rates are correlated with genetic similarity between parents, assessed through DNA fingerprinting, in great reed warblers (*Acrocephalus arundinaceus*, Bensch et al. 1994) and blue tits (*Parus caeruleus*, Kempenaers et al. 1996); for both species, reduced hatching rates are not compensated by increased nestling survival. Darwin's medium ground finches (*Geospiza fortis*) exhibit no effect of inbreeding on a variety of fitness measures including hatching rates and nestling survival, although the sample sizes for these analyses are small (5-8 closely related pairs, Gibbs and Grant 1989).

BENEFITS OF INBREEDING

Optimal inbreeding, or optimal outbreeding, is the theory that, in some species, fitness may be increased through intermediate levels of inbreeding (Shields 1983, 1993; Bateson 1983). Examples of the benefits of inbreeding are extremely rare, and its genetic source—epistasis—is not well understood (Pusey and Wolf 1996). Mating of individuals from distinct populations may disrupt intrinsically coadapted gene complexes or coadapted gene complexes supporting local adaptations (Templeton et al. 1986). Disruption of intrinsically coadapted genes has been documented in captive members of species with high rates of karyotypic inversions (*Gazella* spp., Ryder 1987; owl monkeys *Aotus trivirgatus*, de Boer 1982; *Drosophila,* Wallace 1991) while disruption of local adaptations has been shown in salmonids (Bams 1976, Altukhov and Salmenkova 1987, Reisenbichler 1988, Emlen 1991). However, the importance of outbreeding depression for wild birds and mammals remains unclear (Pusey and Wolf 1996).

Potential benefits of inbreeding within a population are virtually unknown. While preference for moderately related mates has been suggested by experiments with Japanese quail (*Coturnix coturnix*, Bateson 1983)and white-footed mice (*Peromyscus leucopus*, Keane 1990)*, increased fitness has yet to be documented. Although epistasis has been invoked as the genetic basis for theoretical benefits of inbreeding within a population (e.g. Shields 1983), it is commonly defined across populations only (e.g. Falconer 1989). Recently, however, Cheverud and Routman (1995) have proposed a new parameterization of epistasis which includes a within-population component.

INBREEDING IN COOPERATIVELY BREEDING BIRDS

Cooperatively breeding birds exhibit delayed and reduced dispersal, two behaviors which increase the opportunities for inbreeding (Woolfenden and Fitzpatrick 1984). Inbreeding varies among species, however: the acorn woodpecker (*Melanerpes formicivorus*), Florida scrub jay (*Aphelocoma coerulescens*), and red-cockaded woodpecker (*Picoides borealis*) exhibit clear inbreeding avoidance behavior and therefore reduced rates of inbreeding (Koenig and Pitelka 1979, Woolfenden and Fitzpatrick 1984, Walters et al. 1988, Chapter 2); in contrast, the pukeko (*Porphyrio p. melanotus*) and green woodhoopoe (*Phoeniculus purpureus*) exhibit little or no inbreeding avoidance behavior and putatively high rates of inbreeding (Craig and Jamieson 1988, DuPlessis 1992).

Inbreeding avoidance in the red-cockaded woodpecker suggests that close inbreeding may be costly, while short dispersal distances (Walters et al. 1988, Chapter 4) increase opportunities

for moderate inbreeding and suggest that inbreeding benefits may be important. To assess the cost of close inbreeding, I test the hypotheses that closely related pairs and highly inbred individuals have lower fitness than unrelated pairs and noninbred individuals. To assess the benefits of moderate inbreeding, I test the hypotheses that moderately related pairs and moderately inbred individuals have higher fitness than unrelated pairs and noninbred individuals. These hypotheses are each tested against the null hypothesis of no effect of inbreeding on fitness.

FREQUENCY OF INBREEDING

Several studies of inbreeding in birds compare the observed frequency of inbreeding with an expected value based on random mating of individuals in the population (van Tierenden and van Noordwijk 1988, Gibbs and Grant 1989, Part 1996). Observed rates of inbreeding do not differ from expected values based on random mating for great tits (van Tierenden and van Noordwijk, 1988) and Darwin's medium ground finches (Gibbs and Grant 1989). However, the decisions to include or exclude certain individuals from the pool of potential mates may have overwhelming influence on the estimated level of inbreeding expected under random mating (van Tierenden and van Noordwijk 1988, Part 1996).

Members of intact pairs that were present in previous years are often excluded from the pool of potential mates (Gibbs and Grant 1989, Part 1996); however, it is unclear how pair status would differentially affect numbers of related and unrelated individuals. Dispersal distance has been identified as a potential factor affecting the relatedness of available mates (van Tierenden and van Noordwijk 1988, Gibbs and Grant 1989, Part 1996), but all studies thus far have included the entire population in the random pool. To illustrate the influence of space on expected and observed inbreeding values, I calculate these values using three spatial scales: within the entire study area, within the four regions of the study area (see Chapter 1), and within small artificially constructed neighborhoods in one region. Further exploration of the relationship between inbreeding and natal dispersal is presented in Chapter 4.

METHODS

STUDY SPECIES, STUDY AREA, AND DATA COLLECTION

Descriptions of the study species, study area, and methods of data collection are presented in Chapter 1 of this thesis and in Walters et al. (1988). Methods specific to the analysis of inbreeding effects are given below.

CALCULATION OF RELATIONSHIPS

Parentage is known because individuals are banded at the nest and limited molecular analysis has shown that putative parents are the actual parents in almost all cases (Haig et al. 1994). I calculated coefficients of kinship (f) and inbreeding coefficients (F) from a pedigree file containing all known parents using the SAS procedure, PROC INBREED (SAS 1995). In cases in which the identity of one or both parents was unknown, I created dummy parents, so that their young would be marked as full siblings. These dummy parents were used only to establish

relationships, especially important for the early years of the pedigree; they were deleted from later analyses. In cases in which both parents were known but no young were produced, I created dummy progeny, so that the relationship between the pair would be recorded. In this way I established the maximum possible number and depth of relationships.

The inbreeding coefficient is the probability that a locus chosen randomly from an individual contains alleles that are identical by descent; by definition, the inbreeding coefficient of an individual is equal to the coefficient of kinship of its parents (Falconer 1989). The coefficients of kinship used here are by necessity minimum estimates of relationship, as all individuals at the start of data collection and those that dispersed into the study area during the course of data collection were assumed to be unrelated. However, this pedigree was built from 16 years of data and is unusually deep for a population of wild birds (e.g. van Noordwijk and Scharloo 1981, Gibbs and Grant 1989). Generation length in this population of woodpeckers is roughly four years (Reed et al. 1988) and so this pedigree contains four generations.

REPRODUCTION OF PAIRS

Closely related pairs are defined as those pairs for which coefficients of kinship are greater than 0.1. This category includes relationships such as full siblings, half siblings, parent-offspring, aunt-nephew, etc. Unrelated pairs are those for which the detected coefficients of kinship are equal to 0.0. Because no relationships were detected in the population prior to 1984, the years 1980-1983 were deleted from the analyses.

Moderately related pairs are those for which the estimated coefficients of kinship is greater than 0.0 but less than 0.1. Relationships in this category include first and second cousins and more distant relationships. There were no statistical differences between first and second cousins ($0.03 < f < 0.1$) and more distant relationships ($0.0 < f < .03$) for any fitness measure, and so these categories of kinship were combined.

I tested for costs and benefits of inbreeding using the following fitness measures:
1) nest attempts
2) nest failures
3) number of eggs per pair-year
4) number of nestlings per pair-year
5) number of fledglings per pair-year
6) number of one year-old young per pair-year
7) proportion of eggs that hatch (nestlings/eggs)
8) proportion of eggs that fledge (fledglings/eggs)
9) proportion of nestlings that fledge (fledglings/nestlings)
10) proportion of fledglings that survive to one year
    (one year-olds/fledglings).

For the first two measures, each pair's annual reproductive status was used. A nest was attempted if eggs were present, and a nest failed if eggs were present but no fledglings were

produced. Each pair may have appeared in the data more than once, and observations were not independent. For measures 3-10, counts were subtracted from the annual means for that measure to correct for annual variation. These deviations were then summed by pair and divided by the number of observations for each pair. Thus, pairs appeared only once in the data for the analyses of measures 3-10. Measures 3-10 were also analyzed without correcting for annual variation for comparison; results of the two methods were almost identical. Only results produced after correcting for annual variation are reported here.

Proportional fitness measures (measures 7-10) were calculated as follows: the proportion was calculated for each pair in each year, subtracted from the annual mean for that proportion, and deviations were averaged by pair.

Red-cockaded woodpeckers may renest if the first attempt fails, but almost never renest if the first attempt is successful. Only first attempts for which the clutch size was known precisely were included in the calculation of all fitness measures except the number of one year-olds per pair-year and the proportion of fledglings that survive to one year. Pair-years for these measures represent not the number of years the pair exists but rather the number of years the pair attempted a nest and the size of the clutch was known exactly. Annual means were calculated from pairs meeting the same criteria.

In the analyses of the number of one year-olds per pair-year and the proportion of fledglings that survived to one year, reproduction from first and second attempts were included, as were nests for which clutch size is unknown. These last two measures included reproduction only through 1994, as 1995 data were needed to estimate survival. Pair-years for these measures represent the number of years the pair attempted to nest, regardless of success. These fitness measures and levels of inbreeding are similar to but not exactly the same as those used by Gibbs and Grant (1989).

REPRODUCTION OF INBRED INDIVIDUALS

I tested for the costs and benefits of inbreeding for inbred individuals using fitness measures and levels of inbreeding similar to those above, although analyses of the reproduction of highly inbred individuals were severely constrained by sample sizes. Effects of inbreeding on the reproduction of inbred individuals may differ between the sexes, but I was unable to test for this because of small samples. Fitness measures for individuals were calculated from the total counts, corrected for annual variation, summed by individual and divided by the number of years that the individual held a breeding position on a territory (N=882 individuals, mean years=2.70, median=2, max=11, min=1). Years in which a nest was not attempted and years in which clutch size was inferred rather than precisely known were included to retain sample sizes.

I also analyzed the effect of inbreeding on the recruitment of female fledglings into the breeding population. This test was not performed for recruitment of male fledglings because, unlike females, many males become helpers and delay reproduction for one to many years. This delayed reproduction reduces sample sizes for male recruitment considerably.

All statistical tests are identified as results are presented. No fitness measure was normally or symmetrically distributed (normality: Shapiro-Wilks tests, $p<0.10$; symmetry: visual assessment); therefore, the median test was used to detect a location difference between the distributions of two samples. Because I hypothesized directional change in fitness, all two-sample tests were one-tailed.

EXPECTED AND OBSERVED FREQUENCIES OF INBREEDING

To calculate expected levels of inbreeding based on random mating, I used computer simulations of pairing between individuals following the approach of van Tienderen and van Noordwijk (1988), Gibbs and Grant (1989), and Part (1996). These calculations were restricted to individuals in the population in 1995 only, because the ability to detect kinship between individuals was highest for this final year of data.

I calculated observed and expected values for three analyses. For the first analysis, I included all adult males and females present on territories in 1995 within the entire study area. Males and females were randomly paired and the mean coefficient of kinship of these pairs was calculated. This process was repeated 50 times to generate a distribution of expected kinship values; the mean of this distribution was then compared to the mean of observed inbreeding.

Using the same iterative method to generate expected values, I compared mean expected and observed kinship frequencies for four regions within the study area (see Chapter 1) and for artificially designated neighborhoods within one region (Southern Pines). Each of the 37 territories within Southern Pines was the center of a neighborhood; each neighborhood consisted of all territories within a circle with a radius of 2 kilometers. Thus individual territories belonged to more than one neighborhood.

RESULTS

REPRODUCTION OF RELATED PAIRS

Nest attempts and nest failures

Moderately related pairs attempted to nest significantly less than unrelated pairs, and closely related pairs exhibited a marginally significant reduction in nest attempts compared to unrelated pairs (Table 3.1). In contrast, relatedness of the breeding pair had no effect on nest failure (Table 3.1).

Table 3.1. Frequency of nesting attempts and nest failures by the level of relatedness of the breeding pair. Expected values are given in parentheses.

	Did not attempt	Did attempt	x^2	p-value[1]
f=0	232 (245)	1827 (1813)	3.5	0.06
f>0.1	13 (8)	57 (62)		
f=0	232 (245)	1827 (1813)	4.8	0.03
0<f<0.1	29 (20)	143 (152)		
	Did not fail	Did fail		
f=0	1414 (1409)	413 (418)	2.5	0.11
f>0.1	39 (44)	18 (13)		
f=0	1414 (1419)	413 (408)	1.1	0.30
0<f<0.1	116 (111)	27 (32)		

[1]Chi-square tests, df=1.

Costs of inbreeding

Closely related pairs suffered significant inbreeding depression in hatching rates and marginally significant inbreeding depression in the survival of fledglings (Table 3.2). The effect of reduced hatching rates was carried through all life stages: number of nestlings, number of fledglings, and number of one year-old young were all significantly reduced for closely related pairs. The proportion of eggs that fledge was marginally significant, a result consistent with lowered hatching rates. Nestling survival (the proportion of nestlings that fledge) was not affected by inbreeding, nor did it compensate for lowered hatching rates. A separate effect on the survival of fledglings was suggested by the marginally significant reduction for closely related pairs in the proportion of fledglings that survive to age one, and this was consistent with the significant reduction in the number of one year-olds produced by closely related pairs.

Table 3.2. Fitness of closely related (f>0.1) vs. unrelated (f=0) pairs: mean deviation of the pair from annual mean.

	Mean deviation				
Fitness measure	unrelated	closely related	S	Z	p>Z[1]
eggs/pair-year[2]	-0.0440	-0.0952	12.0	-0.40	>0.10
nestlings/pair-year[2]	-0.0538	-0.4421	8.0	-2.00	0.02
fledglings/pair-year[2]	-0.0754	-0.3977	8.9	-1.66	0.05
one year-olds/pair-year[3]	-0.0434	-0.3436	6.0	-1.99	0.02
proportion of eggs that hatch[2]	-0.0053	-0.0945	7.3	-2.25	0.01
proportion of eggs that fledge[2]	-0.0149	-0.0935	9.0	-1.59	0.06
proportion of nestlings that fledge[4]	-0.0124	-0.0445	14.0	0.85	>0.10
proportion of fledglings that survive to one year[3]	-0.0059	-0.1122	7.0	-1.56	0.06

[1]2-sample median test, one-tailed, normal approximation.
[2]N=758 unrelated pairs, 26 closely related pairs: including first attempts only, known clutches only, and nest failures.
[3]N=767 unrelated pairs, 21 closely related pairs: including only nests that fledged at least one young (first or subsequent attempts); 1995 omitted.
[4]N=725 unrelated pairs, 24 closely related pairs: including first attempts only, known clutches only, and only nests with nestlings.

Nest failures were included in the samples for tests of five fitness variables: eggs per pair-year, nestlings per pair-year, fledglings per pair-year, proportion of eggs that hatch, and proportion of eggs that fledge. These variables were tested again with nest failures excluded, and results did not change. For 666 unrelated pairs and 20 closely related pairs, eggs per pair-year was not significantly different, but nestlings per pair-year, fledglings per pair-year, and the proportion of eggs that hatch were significantly lower for closely related pairs, and the proportion of eggs that fledge was marginally lower for closely related pairs.

Closely related pairs remain intact for a marginally significantly shorter period than do unrelated pairs (median test, n=758 unrelated, 26 closely related pairs, X^2=3.5, df=1, p=0.06). Closely related pairs were intact for a mean of 1.35 years, and unrelated pairs were intact for a mean of 1.67 years. However, the reduction in fitness of closely related pairs (Table 3.2) remained unchanged when the samples were restricted to pairs intact for one year only (443 unrelated pairs, 20 closely related pairs).

Benefits of inbreeding

Moderately related pairs showed significant increase in hatching rates which may be carried through until fledging (Table 3.3). This benefit of moderate inbreeding did not translate into significantly greater young, however; although there was a trend for greater numbers of fledglings per pair-year there was no difference in the number of one year-old young (Table 3.3).

Table 3.3. Fitness of moderately related (0<f<0.1) vs. unrelated (f=0) pairs: mean deviation of the pair from annual mean.

fitness measure	mean unrelated	moderately related	S	Z	p>Z[1]
eggs/pair-year[2]	−0.0440	−0.0226	33.0	−0.50	>0.10
nestlings/pair-year[2]	−0.0538	0.0994	39.1	1.02	>0.10
fledglings/pair-year[2]	−0.0754	0.0340	41.3	1.57	0.06
one year-olds/pair-year[3]	−0.0434	−0.0417	30.5	0.54	>0.10
proportion of eggs that hatch[2]	−0.0053	0.0430	43.0	2.00	0.02
proportion of eggs that fledge[2]	−0.0149	0.0149	42.0	1.75	0.04
proportion of nestlings that fledge[4]	−0.0124	−0.0187	34.1	0.16	>0.10
proportion of fledglings that survive to one year[3]	−0.0059	−0.0251	23.0	−1.52	>0.10

[1]2-sample median test, one-tailed, normal approximation.
[2]N=758 unrelated pairs, 70 moderately related pairs: including first attempts only, known clutches only, and nest failures.
[3]N=767 unrelated pairs, 57 moderately related pairs: including only nests that fledged at least one young (first or subsequent attempts); 1995 omitted.
[4]N=725 unrelated pairs, 67 moderately related pairs: including first attempts only, known clutches only, and only nests with nestlings.

When nest failures were excluded from analyses of five fitness measures, results changed somewhat. For 666 unrelated and 59 moderately related pairs, there was no significant difference in eggs per pair year, fledglings per pair-year, or proportion of eggs that hatch; a marginally significant difference in nestlings per pair-year; and a highly significant difference in the proportion

of eggs that fledge. Increased hatching appears to be a true effect, but the data were highly variable.

Pictorial summaries of the difference in reproduction among closely related, moderately related, and unrelated pairs (Tables 3.2 and 3.3) are presented in Figure 3.1 (counts) and Figure 3.2 (proportions). Note that the difference in reproduction of closely related pairs and moderately related pairs was not tested; each was compared to that of unrelated pairs only.
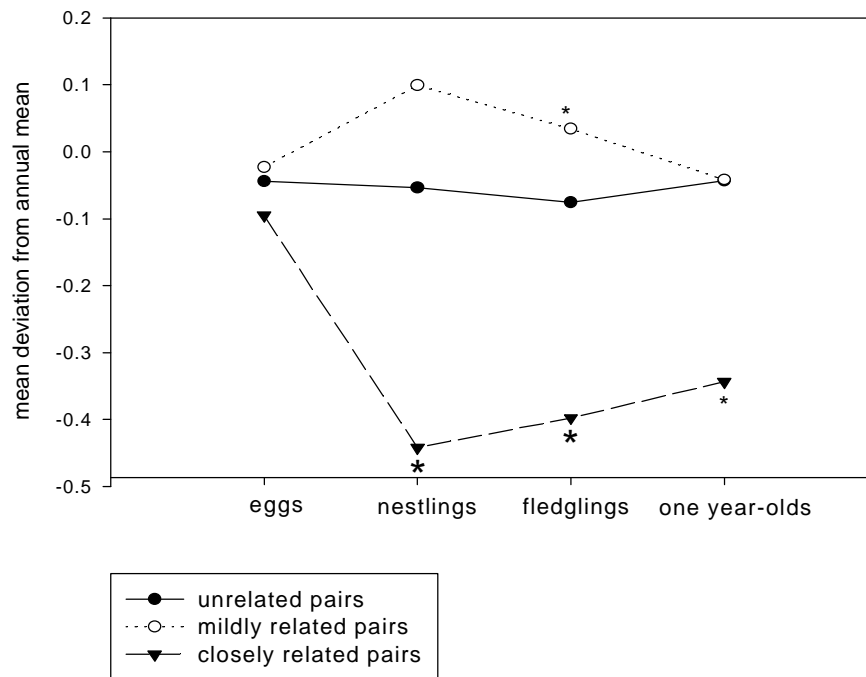
Figure 3.1. Reproduction of closely related and moderately related pairs compared to that of unrelated pairs for fitness measures using counts, in mean deviation of the pair from annual means. Large asterisks indicate a significant difference (p<=0.05) from the value for unrelated pairs; small asterisks indicate a marginally significant difference (0.05<p<0.10).
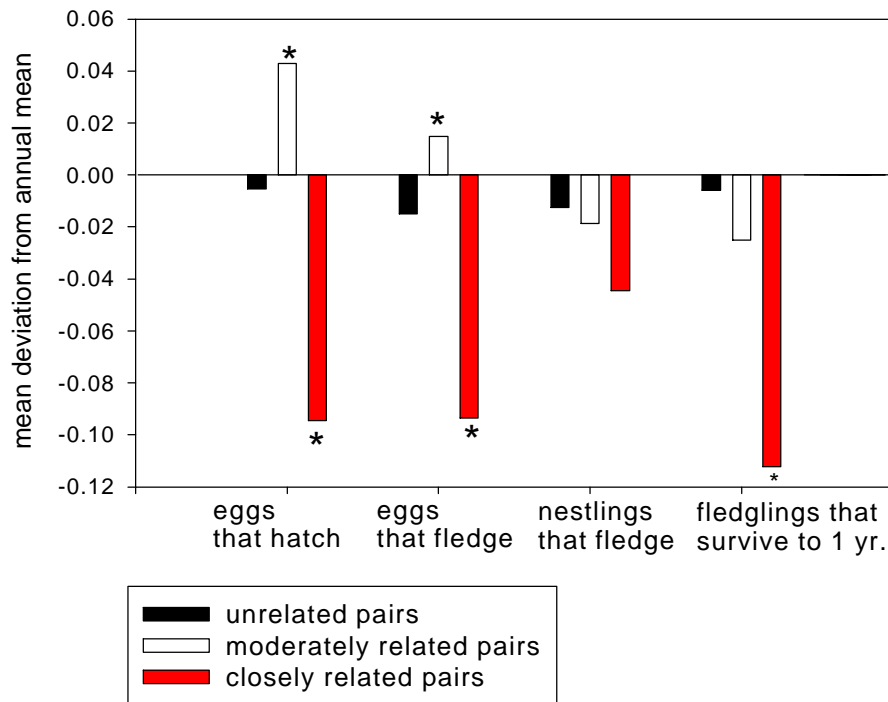
Figure 3.2. Reproduction of closely related and moderately related pairs compared to that of unrelated pairs for proportional fitness measures, in mean deviation of the pair from annual means. Large asterisks indicate a significant difference (p<0.05) from the value for unrelated pairs; small asterisks indicate a marginally significant difference (0.05<p<0.10).

REPRODUCTION OF INBRED INDIVIDUALS

Analyses of the reproduction of inbred individuals was constrained by small sample sizes, as few highly inbred animals were recruited into the breeding population. There were 4 highly inbred females, 8 highly inbred males, 27 moderately inbred females and 12 moderately inbred males occupying breeding positions in the study area during 1984-1995.

Costs of inbreeding

Highly inbred individuals suffered a marginally significant reduction in the proportion of eggs that hatch and a significant reduction in the number of nestlings produced (Table 3.4); these two measures were also significantly reduced in the reproduction of closely related pairs (Table 3.2). No other fitness measure exhibited significant change with inbreeding of the individual (Table 3.4).

Table 3.4. Fitness of highly inbred vs. noninbred individuals: mean deviation of the individual from annual mean.

fitness measure	Mean deviation		S	Z	p>Z[1]
	noninbred	highly inbred			
eggs/year[2]	-0.0618	-0.0304	3.0	-0.71	>0.10
nestlings/year[2]	-0.0844	-0.5294	1.0	-2.14	0.02
fledglings/year[2]	-0.0931	-0.3548	4.0	0.00	>0.10
one year-olds/year[3]	-0.0485	-0.2780	2.0	-0.82	>0.10
proportion of eggs that hatch[2]	-0.0028	-0.1478	2.0	-1.42	0.08
proportion of eggs that fledge[2]	-0.0170	-0.1342	3.0	-0.71	>0.10
proportion of nestlings that fledge[4]	-0.0206	-0.0077	4.0	0.38	>0.10
proportion of fledglings that survive to one year[3]	-0.0095	-0.1522	2.0	-0.82	>0.10

[1]2-sample median test, one-tailed, normal approximation.
[2]N=801 noninbred individuals, 8 highly inbred individuals: including all first attempts with known or inferred clutches.
[3]N=693 noninbred individuals, 6 highly inbred individuals: including first or second nests that fledged at least one young, 1995 omitted.
[4]N=793 noninbred individuals, 7 highly inbred individuals: including all first attempts with known or inferred clutches that produced at least one nestling.

Benefits of inbreeding

Moderately inbred individuals had significantly more eggs that hatch and marginally significantly more eggs that fledge than did noninbred individuals (Table 3.5). These results are fairly consistent with the benefits of inbreeding for moderately related pairs (Table 3.3).

Table 3.5. Fitness of moderately inbred vs. noninbred individuals: mean deviation of the individual from annual mean.

fitness measure	mean		S	Z	p>Z[1]
	level 1	level 2			
eggs/pair-year[2]	-0.0618	-0.0848	16.0	-0.34	>0.10
nestlings/pair-year[2]	-0.0844	-0.0645	17.0	0.01	>0.10
fledglings/pair-year[2]	-0.0931	-0.0641	22.0	0.82	>0.10
one year-olds/pair-year[3]	-0.0485	-0.1329	10.0	0.23	>0.10
proportion of eggs that hatch[4]	-0.0028	0.0173	22.0	1.77	0.04
proportion of eggs that fledge[4]	-0.0170	0.0164	21.0	1.41	0.08
proportion of nestlings that fledge[5]	-0.0206	0.0086	18.0	0.73	>0.10
proportion of fledglings that survive to one year[3]	-0.0095	-0.0207	10.0	0.47	>0.10

[1]2-sample median test, one-tailed, normal approximation.
[2]N=801 noninbred individuals, 34 moderately inbred individuals: including all first attempts with known or inferred clutches.
[3]N=693 noninbred individuals, 19 moderately inbred individuals: including first or second nests that fledged at least one young, 1995 omitted.
[4]N=793 noninbred individuals, 32 moderately inbred individuals: including all first attempts with known or inferred clutches that produced at least one nestling.

Recruitment of female fledglings

Highly inbred female fledglings became breeders fewer times than expected, and there was no difference in recruitment of moderately inbred and non-inbred female fledglings (Table 3.6).

Female fledglings that disappeared either died or dispersed off the study area. Levels of inbreeding probably do not affect dispersal rates, and so the differential recruitment of female fledglings shown in Table 3.6 presumably reflects differential mortality. This result is consistent with earlier analyses revealing a trend toward lowered survival of the young of closely related pairs, and no increase in the number of young produced by moderately related pairs.

Table 3.6. Recruitment of female fledglings by level of inbreeding. Expected frequencies are given in parentheses.

	Became breeder	Disappeared	X^2	p-value[1]
F=0	465 (451)	976 (989)	2.45	0.12
0<F<0.1	27 (33)	81 (74)		
F=0	465 (451)	976 (989)	6.04	0.01
F>0.1	4 (11)	29 (23)		

[1]Chi-square tests, df=1.

FREQUENCY OF INBREEDING

Of all 204 pairs in the study area in 1995, 5.9 percent were closely related, 12.3 percent were moderately related, and 82.8 percent were unrelated. The distribution of actual values and the depth of the pedigree is illustrated in Figure 3.3. The mean of the expected values of average kinship among 204 pairs, based on 50 simulations of random pairing of all individuals, was 0.0025; this was significantly lower than the observed value of 0.0110 (Figure 3.4, two-tailed t-test, n=50, t=-52.07, p=0.0000).

For three of four regions within the study site, the mean of expected values generated from 50 simulations of random pairing of all breeding adults within each region was significantly lower than the observed value (Figure 3.5; t-tests: FB, expected=0.0034, observed=0.0051, n=50, t=-4.35; MIN, expected=0.0058, observed=0.0060, n=50, t=-0.19, p=0.12; SGL, expected=0.0133, observed=0.0176, n=50, t=-5.32, p=0.0000; SOPI, expected=0.0147, observed=0.0171, n=50, t=-2.02, p=0.043). Each expected and observed mean was calculated from the following number of pairs: FB, n=82; MIN, n=26; SGL, n=59; and SOPI, n=37.
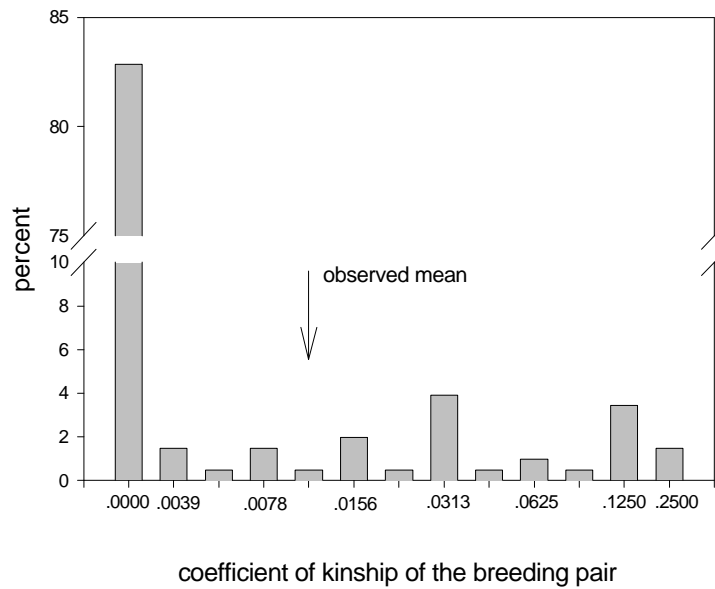
Figure 3.3. Actual detected inbreeding among all pairs (n=204) in the study area in 1995. Note the y-axis is broken and the x-axis is not to scale.
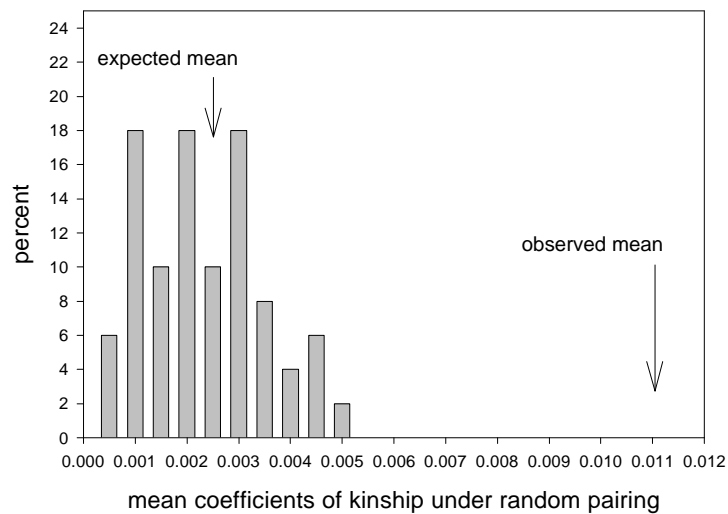
Figure 3.4. Distribution of the mean coefficients of kinship between pairs from 50 rounds of random pairing of all adults occupying breeding positions in the study area in 1995. The observed and expected means are indicated.
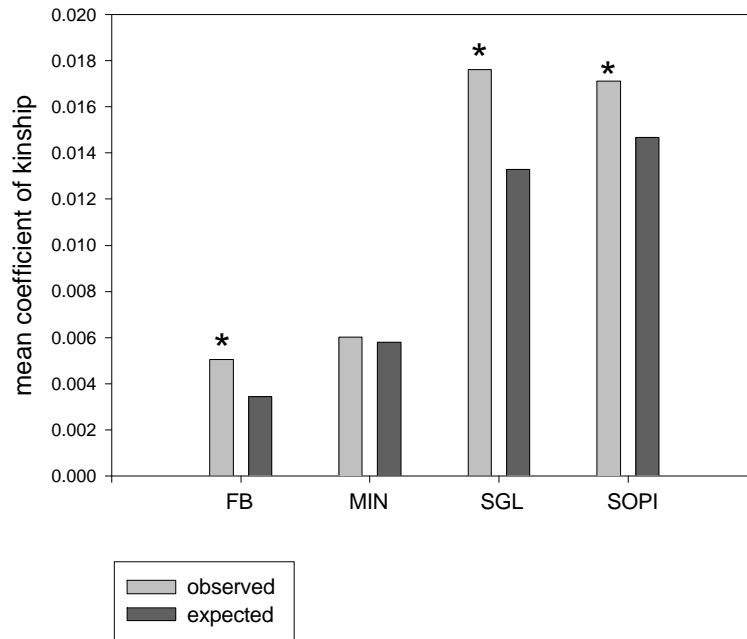
Figure 3.5. Observed and expected mean coefficients of kinship for four regions within the study area. Asterisks indicate observed frequencies that were significantly different from the expected value.

Observed inbreeding differed significantly across regions, as Figure 3.5 suggests (one-way median test, X^2=10.21, df=3, p=0.017). Mean kinship of pairs was higher in the Sandhills Game Lands (SGL) and Southern Pines (SOPI) than in Fort Bragg (FB) and the minor sites (MIN). This increase in kinship in the Game Lands and Southern Pines appears to consist of a proportional increase in both closely related and moderately related pairs (Table 3.7). No statistics were performed on these frequencies because of low cell sample size. The depth of the pedigree for Southern Pines and the Game Lands is one year greater than that of Fort Bragg and one to three years greater than that of the minor sites. In addition, both Southern Pines and the Game Lands contain considerably fewer groups than Fort Bragg (37 and 59 vs. 82, respectively) although the minor sites contain the fewest number of groups (26).

Within small, artificially designated neighborhoods in Southern Pines, the expected kinship among breeding pairs, generated from 50 simulations of random pairing of breeding individuals within neighborhoods, was significantly greater than the observed value. For this analysis, I

combined the differences between expected and observed values for all 37 neighborhoods; the mean of these differences was significantly greater than zero (sign test, N=37, mean difference=0.0038, test statistic M=3.8, p=0.035). The number of territories in each neighborhood ranged from 3 to 12, observed inbreeding within neighborhoods ranged from 0 to 0.1250 (SOPI 018), and expected inbreeding within neighborhoods ranged from 0 to 0.1018 (SOPI 018). Because territories may appear in more than one neighborhood, neighborhoods are not independent; therefore, these results are not definitive.

Table 3.7. Percentages of closely related, moderately related, and unrelated pairs within four regions of the study area. Actual frequencies are in parentheses.

Region	unrelated	moderately related	closely related	total
FB	90.3% (74)	7.3% (6)	2.4% (2)	(82)
MIN	92.3 (24)	3.8 (1)	3.8 (1)	(26)
SGL	72.9 (43)	20.3 (12)	6.8 (4)	(59)
SOPI	75.7 (28)	16.2 (6)	8.1 (3)	(37)

DISCUSSION

I clearly demonstrate inbreeding depression for closely related pairs of red-cockaded woodpeckers. This result is an important contribution to our understanding of inbreeding in wild populations, and it is the first example of inbreeding depression in a species of bird that exhibits inbreeding avoidance behavior. Two separate effects of close inbreeding are revealed: lowered hatching rates and lowered survival and recruitment of young. Hatching rates and number of nestlings may be reduced in the reproduction of inbred individuals, but low sample size leaves these results ambiguous. Additionally, closely related pairs relatives may attempt to nest less often than unrelated pairs.

A second important result of this study is the increase in hatching rates but unaffected or decreased survival of young for moderately related pairs and moderately inbred individuals. Moderately inbred females were recruited into the population at a rate equal to that of non-inbred females. Finally, tests of the frequency of observed inbreeding vs. that expected under random mating suggest population structure, or non-random mating, both within the entire study area and within three regions of the study area. Each of these results is discussed in detail below.

COSTS OF INBREEDING

Lowered hatching rates for closely related pairs and inbred individuals in this population of red-cockaded woodpeckers are consistent with inbreeding effects in domestic birds (Schoffler 1948, for reviews see Woodard et al. 1982 and Flock et al. 1991), great tits (Bulmer 1973, Greenwood et al. 1978, van Noordwijk and Scharloo 1981), blue tits (Kempenaurs et al. 1994),

and great reed warblers (Bensch et al. 1994). Closely related pairs of red-cockaded woodpeckers exhibit reduced hatching rates which are not compensated by increased nestling survival: the effect is carried through all subsequent life stages. Therefore, unlike great tits (van Noordwijk and Scharloo 1981) but like blue tits (Kempenaurs et al. 1994) and great reed warblers (Bensch et al. 1994), the lowered hatching rates revealed here are subject to natural selection and so have evolutionary significance.

The effect of inbreeding on the survival of red-cockaded woodpeckers is revealed in two results: closely related pairs suffer a marginally significant reduction in the proportion of fledglings that survive to one year old, and a significant reduction in the recruitment of female fledglings. The latter analysis is equivalent to the former, because most females begin breeding at one year of age. The only other example of an effect of inbreeding on the survival of wild birds is the drastic reduction in the proportion of inbred song sparrows in an island population subjected to severe winter storms (Keller et al. 1994). The survival effect revealed by Keller et al. (1994) is an example of episodic selection; the survival effect revealed here is evidence of selection applied continuously, at least at the present time.

An additional source of reduced fitness of closely related pairs is the marginally significant reduction in nest attempts. The mechanism behind this decrease in nest attempts was not assessed; however, recognition of familiar kin may be sufficient to explain reduced nest attempts. Pairs consisting of familiar kin accounted for 16 percent of closely related pairs (see below). Differing numbers of nest attempts between closely related and unrelated pairs is evidence of both inbreeding depression and inbreeding avoidance.

If selection can reduce genetic load and the cost of inbreeding (Templeton and Read 1983), why does inbreeding depression persist in this population of woodpeckers? There is no clear evidence that inbreeding reduces inbreeding depression in wild populations of animals (Pusey and Wolf 1996) or in captive birds (e.g. Woodard et al. 1981). Reduced hatching rates persist in a population of the great reed warbler even though the population experienced at least one and possibly several bottlenecks (Bensch et al. 1994). Persistent inbreeding depression may result from assorting or fixed slightly deleterious alleles or from loss of overdominance (Charlesworth and Charlesworth 1987, Hedrick 1994). Alternatively, the frequency or history of inbreeding may not be sufficient to remove severely deleterious alleles. For the red-cockaded woodpecker and other wild species, the genetic basis of inbreeding depression and its relationship to natural selection have yet to be assessed.

BENEFITS OF INBREEDING

Here, both moderately related pairs and moderately inbred individuals exhibit a significant increase in hatching rates; for moderately related pairs, this benefit results in greater numbers of young fledged. The consistency of increased hatching rates across analyses lends credence to this result, but, to my knowledge, there is no precedent or theoretical basis for it in the literature. Studies of inbreeding in wild birds have not assessed the fitness of moderately related pairs separately from that of closely related pairs, and studies of inbreeding in captive and domestic birds have focused on high rates of inbreeding such as continued full-sib matings. The potential

implications of epistasis for non-random matings within a population have not been developed (but see Cheverud and Routman 1995); in fact, the benefit of epistasis across populations has not been clearly documented in wild animals and its importance to evolutionary processes remains obscure (Cheverud and Routman 1995, Pusey and Wolf 1996).

However, in this study, neither moderately related pairs nor moderately inbred individuals produce greater numbers of one year-old young than unrelated pairs or noninbred individuals. Additionally, recruitment of moderately inbred individuals into the breeding population was equal to that of non-inbred individuals. Therefore, any benefit of moderate inbreeding does not appear to be under natural selection at the present time.

Historically, moderate inbreeding may have been under selection. The benefit of increased hatching rate may at one time have been maintained through fledging and recruitment, if the conditions that sub-adults face were somehow different.

That moderately related pairs attempt to nest significantly fewer times than closely related pairs is a puzzling result without clear explanation. No mechanism for actively recognizing moderate kin has been suggested for this species or for birds in general.

EXPECTED AND OBSERVED FREQUENCIES OF INBREEDING

Comparing the observed frequency of inbreeding in a population with that expected under random mating has been identified as an appropriate test for inbreeding avoidance (Ralls et al. 1986, van Tierenden and van Noordwijk 1988, Gibbs and Grant 1989). A conclusion common to those using this approach is that mating is random with respect to kinship (van Tierenden and van Noordwijk 1988, Gibbs and Grant 1989). However, this type of analysis is confounded by dispersal patterns in two ways. First, dispersal patterns may cause unequal probabilities of mating among all individuals (van Tierenden and van Noordwijk 1988); to overcome this difficulty, dispersal throughout the population is either shown (van Tierenden and van Noordwijk 1988) or assumed (Gibbs and Grant 1989). Second, dispersal distance may itself be a mechanism for inbreeding avoidance; if the null model includes all birds within common dispersal range it may then, in fact, include inbreeding avoidance (Part 1996). Thus, comparison of observed and expected inbreeding does not distinguish between dispersal patterns and inbreeding preference or avoidance. Inbreeding avoidance itself may best be tested by observations of the behavior of individuals in the presence and absence of kin (Part 1996 and references within, Chapter 2, Chapter 4, below).

However, this study is unique in that it reveals inbreeding rates significantly different from those expected under random mating. Because no previous study has produced estimates of inbreeding that depart from random expectations, no one has clearly defined the meaning of such departures. Therefore, I propose interpretations for three possible results. If observed inbreeding is equal to the expected frequency, then dispersal is random and/or mating is random with respect to kinship (Part 1996). It then follows that if observed inbreeding is higher than the expected value, dispersal is not random but restricted within the defined area, and/or birds are choosing

related mates. Finally, if observed inbreeding is lower than the expected value, dispersal exists beyond the defined area and/or birds are avoiding related mates.

Here, inbreeding among all breeding birds in the study area and among birds within three of four regions is higher than expected under random mating. Close inbreeding is costly, moderate inbreeding provides no lasting benefit, and short dispersal distances characterize this species; therefore it is likely that, rather than choosing related mates, birds are not dispersing randomly throughout the study area nor throughout three of the four regions within the study area. Short dispersal distances increase the probability of mating with a relative, as relatives are not evenly distributed throughout the population (Chapter 4).

Upon restricting the area included in the generation of expected values to small neighborhoods, observed inbreeding is lower than expected. Dispersal distances may be greater than across these small areas; alternatively, the birds may be actively avoiding mating with kin. It is possible that this difference between observed and expected levels of inbreeding by neighborhood results solely from females avoiding breeding with the closely related males on their natal territories.

To my knowledge, the only other analysis of kinship at this scale was performed by van Tierenden and van Noordwijk (1988) on great tits: they found no difference in the kinship of a pair and that expected if each member of the pair had mated with the opposite sex in the nearest neighboring pair. They concluded that mating was random with respect to kinship.

OBSERVED RATES OF CLOSE INBREEDING

It is difficult to compare observed rates of close inbreeding with those in the literature because they have been calculated in a myriad of ways. The most accurate representation of the rate of close inbreeding in this population of red-cockaded woodpeckers is that 5.9 percent of pairs present in 1995 had coefficients of kinship equal or greater than 0.125. Other studies restrict the definition of close inbreeding to coefficients of kinship greater or equal to 0.25 (e.g. Ralls et al. 1986), and generally include all pairs present during the study period (e.g. Greenwood et al. 1978, Gibbs and Grant 1989). In a review of close inbreeding in wild populations (Ralls et al. 1986), rates of very close inbreeding (f=>0.25) for several species of birds range from 0.0 percent for the white-fronted bee eater (*Merops bullockoides*) to 0.4 percent for the Florida scrub jay, 3.0 percent for the great tit in Vlieland, 3.2 percent for the acorn woodpecker, and 9.8 percent for the mute swan (*Cygnus olor*).[2] Very close inbreeding is estimated at 0.6 percent in one population of Darwin's medium ground finches (Gibbs and Grant 1989) and 0.5 percent in one population of collared flycatchers (*Ficedula albicollis*, Part 1996). Greenwood and Harvey (1978) report 1.6 percent of all pairs of great tits in Wytham Wood had coefficients of kinship greater or equal to 0.125. These authors specified that pairs present in more than one year were included more than once. Probably the highest rate of inbreeding documented to date is within the pukeko; more than 50% of birds engage in matings with parents or siblings (Craig and Jamieson 1988). Comparable figures for this population of red-cockaded woodpeckers are as

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[2] The estimate of 19.4 percent given in Ralls et al. (1986) for the splendid fairy wren (*Malurus splendens*) requires reevaluation because of the extremely high rates of extra-pair copulations since reported (Brooker et al. 1990).

follows: of 1437 unique pairs present during 1984-1995, 1 percent (15) were very closely related ($f \geq .25$) and 2.9 percent (43) were closely related ($f \geq 0.125$). Of 2308 pair-years, 0.9 percent (21) contained pairs that were very closely related and 3.0 percent (70) contained pairs that were closely related.

Thus, the rate of close inbreeding in this population of red-cockaded woodpeckers is similar to those documented for other cooperatively breeding species such as the Florida scrub jay and acorn woodpecker, similar to those documented for non-cooperative breeders such as the great tit, collared flycatcher, and Darwin's medium ground finch, and far below that observed in the polygynandrous, communally breeding pukeko. Such low rates of inbreeding in the red-cockaded woodpecker are surprising given reduced and delayed dispersal, and suggest that inbreeding avoidance mechanisms are important for this species.

INBREEDING AVOIDANCE

Inbreeding avoidance is an important cause of breeding dispersal (Walters et al. 1988, Chapter 2) and undoubtedly reduces the percentage of closely related pairs. However, in light of the inbreeding depression revealed here, it is appropriate to consider the effect the cost of inbreeding may have on natal dispersal. The relationship between inbreeding and dispersal distance of fledglings is explored in Chapter 4; here, I briefly examine the frequency of dispersal of female fledglings and the incidence of close inbreeding.

In the cooperatively breeding red-cockaded woodpecker, it is common for males to inherit the breeding position on the natal territory (Walters et al. 1988), but extremely rare for females to do so: of 1077 females in this population for which natal and first breeding location is known, 11 (1 percent) inherited their natal territory. The rarity of this behavior is probably due to the cost of inbreeding and the philopatry of breeding males. For a female to inherit and not breed with a close relative, several events must occur in close succession: 1) the breeding position must be vacant; that is, the mother must move or die; 2) the father must die (movement of breeding males almost never occurs); and 3) brothers (helpers or fledglings) must not be present, must move, or die (Walters pers. comm.). Of the 11 times a female inherited her natal territory, in 5 cases the mother and father died and there were no helpers present, in 2 cases the mother, father, and helper(s) died, in 3 cases close inbreeding occurred, and in the remaining case the relationship between the subsequent pair was unknown. Incidentally, in all 11 cases the breeding female died; in no case did she move to another breeding location. While these data are anecdotal, the suggestion is that females disperse from natal territories to avoid inbreeding.

THE FORMATION OF CLOSELY RELATED PAIRS

Failure of females to disperse in the presence of a familiar, related breeding male accounted for 16 percent (7 of 43) of closely related pairs: three female fledglings remained on the natal territory to breed with a related male (see above), and four breeding females remained to breed with an inheriting son (Chapter 2). In 84 percent of cases of closely related pairs (36 of 43), dispersal of females occurred. In some cases, more than one dispersal event between two territories led to the formation of closely related pairs; for example, a female disperses, and her

progeny disperses back to their mother's natal territory. In other cases, dispersal among three territories led to the formation of closely related pairs. Dispersal among four territories occurs, but the kinship between pairs formed through this dispersal pattern is rarely above 0.125. Short distance dispersal undoubtedly increases the likelihood that other dispersal events will occur between or among the same territories, and that inbreeding will result.

Kin recognition in this species is thought to be based on familiarity (Walters 1990), although females are also able to discern kin from among familiar males (i.e., females identify which helpers are related, Chapter 2). The processes by which closely related pairs form lends support to the familiarity hypothesis. Pairs between closely related, familiar kin account for 21 percent of closely related pairs: this proportion includes the dispersal failures noted above and an additional 2 cases in which full sibs from the same nest dispersed to the same territory after an intervening period of at least one year. All other closely related pairs had no familiarity prior to the breeding event.

INBREEDING WITHIN REGIONS

I document significantly different rates of inbreeding among the four regions of our study area: red-cockaded woodpeckers have lower rates of inbreeding in Fort Bragg and the minor sites than in the Sandhills Game Lands and Southern Pines. These results are consistent with the electrophoretic survey performed by Stangel et al. (1992), through which the authors found that heterozygosity in the Game Lands is approximately half that of Fort Bragg. (Woodpeckers in the minor sites and Southern Pines were not included in the survey.)

The cause of this inequality may be geography. The Game Lands is a relatively isolated region within the study area; Southern Pines is somewhat isolated, and Fort Bragg and the minor sites occupy more centralized locations. Other factors include the difference of a year in the depth of the pedigrees for the Game Lands, Southern Pines, and Fort Bragg, and the fewer number of birds in the first two regions than in Fort Bragg. The minor sites have the fewest number of birds, but also the shortest pedigree. In addition, the minor sites contain aggregations of groups which are fairly separate from each other; the other regions are more easily identifiable as a cohesive unit, at least at the present time.

IMPLICATIONS FOR CONSERVATION

Costs of inbreeding in this population do not appear unless inbreeding is high ($f >= 0.125$). However, extremely small isolated populations do exist, and inbreeding depression may well be one of many threats to the viability of such severely reduced populations. Conservation of small populations is important for the retention of genetic variability (Stangel et al. 1992); the population differentiation illustrated here and elsewhere (Stangel et al. 1992) implies that populations may be locally adapted and genetically distinct. Recovery of the species would be facilitated by the availability of locally adapted genomes.

FURTHER RESEARCH

Virtually all aspects of inbreeding in wild populations require further research before a general theory can be formulated, but increasing accumulation of long-term data will quicken our progress. Especially needed are studies which assess the potential costs and benefits of high and intermediate levels of inbreeding separately. Of equal importance is experimental research into the relative importance of epistasis, overdominance, and partial dominance for various species and populations. The synthesis of recent metapopulation models with frequencies and costs of inbreeding is an exciting prospect with great import for both evolution and conservation.

CHAPTER 4: NATAL DISPERSAL, KINSHIP, AND INBREEDING

INTRODUCTION

Natal dispersal, the movement of individuals between natal and breeding locations, is a critical life-history component for all taxa. Natal dispersal controls gene flow and population structure (Wright 1977, Barrowclough 1980). It also affects species distributions, demographics, population regulation, and population viability (Greenwood 1980, Harrison et al. 1988, Pulliam 1988). Two of the factors that may affect natal dispersal are inbreeding avoidance (reviewed by Pusey 1987, Pusey and Wolf 1996) and optimal inbreeding (Shields 1982, 1983). Potentially, both factors may be in effect at the same time.

Natal dispersal patterns which serve to prevent close inbreeding have been documented in several species of mammals and birds (Packer 1979, Pusey 1980, Woolfenden and Fitzpatrick 1984). However, whether these patterns have evolved as mechanisms for avoiding inbreeding costs has been debated (reviewed by Pusey 1987, Pusey and Wolf 1996). To clearly show the influence of inbreeding avoidance on dispersal, fitness costs of close inbreeding must first be documented. Then, the researcher must reveal either 1) a change in dispersal behavior in the presence or absence of close relatives, or 2) a predictable kinship structure, or distribution of close relatives in space, and dispersal distances sufficient to avoid mating with close relatives.

Optimal inbreeding refers to the potential fitness benefits of mating with moderately related individuals such as first cousins (Shields 1982, 1983, Bateson 1983). Natal dispersal behavior that serves to promote breeding with moderately related individuals remains a theoretical construct that has not been documented in wild populations, and evidence of the fitness benefits of moderate inbreeding is scarce as well. Documenting the effect of optimal inbreeding on dispersal requires steps similar to those described above. It is necessary to first show fitness benefits of moderate inbreeding, and then to reveal either changing dispersal behavior in the presence of moderate relatives or a predictable distribution of such relatives in space coupled with dispersal distances that promote the likelihood of mating with moderately related individuals.

In this study, I test for effects of inbreeding avoidance and optimal inbreeding on natal dispersal within a population of the red-cockaded woodpecker (*Picoides borealis*). The first step in revealing inbreeding avoidance or optimal inbreeding was completed prior to this study. Close inbreeding results in significant fitness costs: closely related pairs (f>0.1) suffer significantly reduced hatching rates and production of fledglings and recruits (Chapter 3). Moderate inbreeding produces some benefits, but these benefits may not be under selection: moderately related pairs (0<f<0.1) exhibit significantly increased hatching rates, but no increase in numbers of recruits produced (Chapter 3).

Here, I give a detailed description of natal dispersal within this population. Next, I examine the kinship structure of the population to determine whether dispersal distances promote moderate inbreeding and/or serve to avoid close inbreeding. I then perform a series of tests for

changes in dispersal behavior in the presence of kin. The first assesses the effect of close relatives, present on the natal territory, on the frequency of dispersal. Subsequent tests assess the effects of relatives near the natal territory on natal dispersal distance. Finally, I examine whether kinship of potential mates affects the frequency with which nearest vacancies are occupied.

METHODS

STUDY SPECIES

The red-cockaded woodpecker is an endangered, cooperatively breeding species endemic to the pine savannas of the southeastern United States. Roughly half of fledgling males delay dispersal and remain on the natal territories as helpers, while almost all fledgling females disperse (Walters et al. 1988). Helper males commonly acquire a breeding position in their natal or neighboring territory, and dispersing males may acquire a breeding position, or, more rarely, become floaters until a breeding position is obtained (Walters et al. 1988). Dispersing females may become breeders or floaters, but do not occupy territories without an adult male (Walters et al. 1988).

Delayed dispersal of males of this species has been well-researched (Walters et al. 1992, Lennartz et al. 1987), but factors influencing the natal dispersal of females have not been assessed. Understanding these factors is important, however, because movement of females is critical to maintaining actively breeding groups (Walters et al. 1988), and it is the number of actively breeding groups which determines population growth or decline in this species (Walters 1991). Therefore, I restrict my tests of inbreeding avoidance and optimal inbreeding to the natal dispersal of females.

STUDY AREA AND METHODS OF DATA COLLECTION

The study area is located in the Sandhills of south-central North Carolina, and encompasses over 110,000 ha. Dominant vegetation is second-growth longleaf pine, with a midstory of scrub oaks (Quercus spp.) and a ground cover of wiregrass (*Aristida stricta*). All woodpecker groups within the study area (roughly 220) are monitored. Additional groups, not monitored by this project, occur to the south and east of the study area.

Data collection began in 1980 and continues through the present. Individuals were banded with a unique color combination and reproduction of all groups was monitored. Most birds were banded as nestlings, and each breeding season all members of each group were identified. Breeding status was assigned based on behavioral observations and/or the relative ages of birds present, and group affiliation was assigned through behavioral observations and roost checks. Sex was determined by the presence of a red crown patch in males during their first fall, or by the presence of the red cockade in adult males, verified by capture. Therefore, parentage and placement of most individuals was known. Further information concerning the study species, study area, and methods of data collection is given by Walters et al. (1988) and Carter et al. (1983).

DEFINITIONS OF MEASURES

Natal dispersal distance

I calculated dispersal distances in units of territories crossed and kilometers for over 1000 individuals with known birth and breeding locations between 1982 and 1995. These data were partitioned by sex and life-history strategy of one year-old individuals (i.e., helper, floater, disperser). Movements of individuals in groups that changed territories together were excluded because they probably reflect ambiguities in site classification rather than true dispersal.

Data collected during regular nest-monitoring and censusing activities included locations of foraging or congregating adults in universal transverse mercator (UTM) coordinates. Territory centers were then estimated by the centroid of the polygon including all these location points pooled over 13 years (1980-1992). For the few new territories created between 1993 and 1995, UTM coordinates of nest trees were used to estimate territory centers.

Dispersal distance in kilometers was the length of the straight line between estimated territory centers. Dispersal distance in the number of territories crossed was a count of territories whose centers were within 400 meters of this straight dispersal line. For this measure the original territory was not counted but the receiving territory was, so that a bird moving next door crossed 1 territory and a bird remaining in the original territory crossed 0 territories. I counted only territories occupied in the year the female appeared in the new location. Unoccupied sites were not considered territories, in part because females do not remain in sites that have no male present.

Kinship

Kinship was calculated using the SAS procedure, PROC INBREED (SAS 1995), and a pedigree file containing all known parents from 1980-1995. Parentage is known because individuals are banded at the nest and limited molecular analysis has shown that putative parents are the actual parents in almost all cases (Haig et al. 1994). The SAS procedure calculates coefficients of kinship (the probability that corresponding alleles chosen at random are identical by descent) for both existing pairs and hypothetical matings. Estimates of kinship were minimum estimates, because all individuals at the start of data collection and those that dispersed into the study area during the course of data collection were assumed to be unrelated. However, this pedigree is unusual in studies of wild populations because it contains as many as four generations (four years per generation, Reed et al. 1988).

Natal and breeding neighborhoods

I constructed a neighborhood for each territory for use in subsequent analyses. A neighborhood was defined as all territories whose centers were within two kilometers of the center of the territory in question. The selection of two kilometers as the appropriate distance was arbitrary. Neither the natal territory nor the breeding territory were included in the neighborhoods.

SPATIAL DISTRIBUTION OF KIN

The spatial distribution of moderately and closely related males in this population was analyzed in two ways. First, I compared the proportion of related breeding males in the neighborhood of a one year-old breeding female to the distance that female dispersed. A negative correlation between dispersal distance and the proportion of kin neighboring the breeding female would reveal clustering of kin near the natal site. This test was restricted to females that dispersed and bred as one year-olds in 1993, 1994, and 1995. Females that did not breed as one year-olds were excluded because any effect of male kin present during the years these females did not breed was not easily tested. I restricted the sample to three years of data to reduce computer-intensive calculations of kinship and neighborhoods, and chose the most recent years in the data set because the detection of kinship, especially at low levels, increases as the pedigree grows. There were 112 one year-old breeding females with known dispersal distance in 1993, 1994, and 1995 combined. Only 109 of these females appeared in the analyses of neighborhoods because in three instances, the neighborhood contained only the natal and breeding site.

Second, I tested for differences in dispersal distances of females with moderately and closely related mates and those with unrelated mates. Shorter dispersal distances for females with related mates would suggest non-random distribution of kin. The sample for this test was all females that dispersed and bred as one year-olds between 1982 and 1995. It is important to note that these and subsequent analyses were confined to the area within female dispersal range; in other words, because I used actual dispersal distances in my analyses, the kinship of males outside the range of female dispersal was not assessed.

CHANGE IN THE FREQUENCY OF DISPERSAL FROM THE NATAL SITE

I compared the dispersal behavior of fledgling females with and without the possibility of close inbreeding on the natal territory. I included only those cases, 1980-1995, in which the fledglings' mother was no longer present in the following year and there was an adult male present, so that the opportunity to breed in the natal territory existed. I judged that there was a possibility of close inbreeding if any male present on the territory in the year the female was born—including her father, fledgling brothers, or any helper—was the breeding male in the following year. Any helper on the natal territory was assumed to be closely related, because over 80 percent of helpers are full or half-sibs of the young they help raise (Walters et al. 1988). I then tested the association of close inbreeding with frequency of dispersal from the natal site, but because there is rarely no chance of inbreeding, sample size for this test is small.

CHANGE IN NATAL DISPERSAL DISTANCE

Change in natal dispersal distance in the presence of moderately or closely related males was analyzed in two ways. First, I compared dispersal distances of females with the proportion of related males in the neighborhood of the female's natal territory. Second, I identified vacancies available to the dispersing female, and tested for differences in dispersal distance between females with and without related males occupying those territories with vacancies. Females included in these two tests were those that dispersed and bred in their first year, between 1993 and 1995, for reasons described above.

KINSHIP AND THE FREQUENCY OF OCCUPYING THE NEAREST VACANCY

My final tests of inbreeding avoidance and optimal inbreeding examined whether or not a female dispersed to the vacancy that is closest to her natal site. I compared the number of times a female dispersed to the closest vacancy with the kinship of the males on these territories. Inbreeding avoidance predicts females occupy the closest vacancies less often if the breeding male there is a close relative; optimal inbreeding predicts that females will occupy the closest territory more often if that male is moderately related. Again, only females that dispersed and bred as one year-olds between 1993 and 1995 were included in this test.

Available vacancies were identified as any territory with a one year-old breeding female or with a solitary male. Vacancies acquired by older females were considered unavailable to one year-olds (because age-based dominance is assumed), and were excluded from all analyses. There were 60, 57, and 64 available vacancies in 1993, 1994, and 1995, respectively.

STATISTICAL TESTS

Statistical tests are identified as analyses are presented. Non-parametric tests were used because data were not normally distributed (Shapiro-Wilks tests, $p<0.10$). Chi-square tests with more than 20% of expected values less than 5 were performed using a continuity correction factor, and are indicated with a subscripted test statistic (X^2_c).

RESULTS

NATAL DISPERSAL DISTANCE

Table 4.1 presents dispersal distance of individuals from their natal to first breeding territories, in kilometers and number of territories crossed, by sex and the life history the individual exhibited as a one year-old. Figures 4.1 and 4.2 present distributions of dispersal distances for all birds and for the most common life histories. The differences in dispersal distances among life histories and between the sexes are significant. Females that were floaters as one year-olds moved significantly farther than females that dispersed and bred in their first year (median tests; n=65,517; kilometers: X^2=21.2, df=1, p=0.0001; territories crossed: X^2=10.3, df=1, p=0.001). Males that dispersed and bred or floated in their first year moved significantly farther than males that helped (n=116,240; kilometers: X^2=94.3, df=1, p=0.0001; territories crossed: X^2=116.9, df=1, p=0.0001). Natal dispersal in this population is clearly sex-biased: females as a group dispersed significantly farther than males (n=603,467; kilometers: X^2=127.1, df=1, p=0.0001; territories crossed: X^2=171.0, df=1, p=0.0001), and females that dispersed and bred or floated as one year-olds moved significantly farther than males exhibiting these same strategies (n=582,76; kilometers: X^2=4.8, df=1, p=0.028; territories crossed: X^2=6.1, df=1, p=0.013).

Table 4.1. Distance traveled by red-cockaded woodpeckers from natal to first breeding location, in kilometers and number of territories crossed, by life history strategy as one year-olds (1982-1995).

| Life history as one year-old	N	Territories crossed			Kilometers		
		median	mean	max	median	mean	max
Female,							
remain and help	8	1.5	1.4	3	1.9	2.5	6.0
remain and breed	8	0	0.0	0	0.0	0.0	0.0
disperse and breed	517	2	2.7	14	3.4	4.6	31.7
disperse, solitary	1	2	2.0	2	3.3	3.3	3.3
disperse and help	4	4	4.0	7	4.2	3.9	6.2
disperse and float	65	3	3.9	11	5.4	7.0	29.9
total, females	603	2	2.8	14	3.6	4.7	31.7
Male,							
remain and help	240	0	0.7	7	0.0	1.0	25.1
inherit and breed	41	0	0.0	0	0.0	0.0	0.0
inherit, solitary	9	0	0.6	2	0.0	0.4	2.2
disperse and breed	76	2	2.4	11	2.6	3.6	15.0
disperse, solitary	36	2	2.4	7	3.5	5.0	20.0
disperse and help	25	2	2.1	6	1.3	2.9	15.0
disperse and float	40	2	3.1	10	4.5	6.6	23.1
total, males	467	1	1.3	11	0.9	2.2	25.1
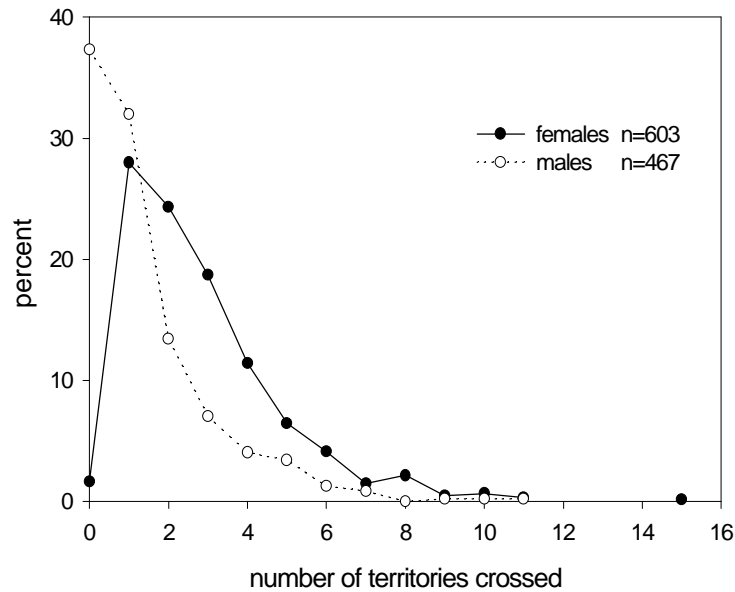
Figure 4.1. Distribution of natal dispersal distances, in number of territories crossed, for all male and female red-cockaded woodpeckers, 1982-1995.
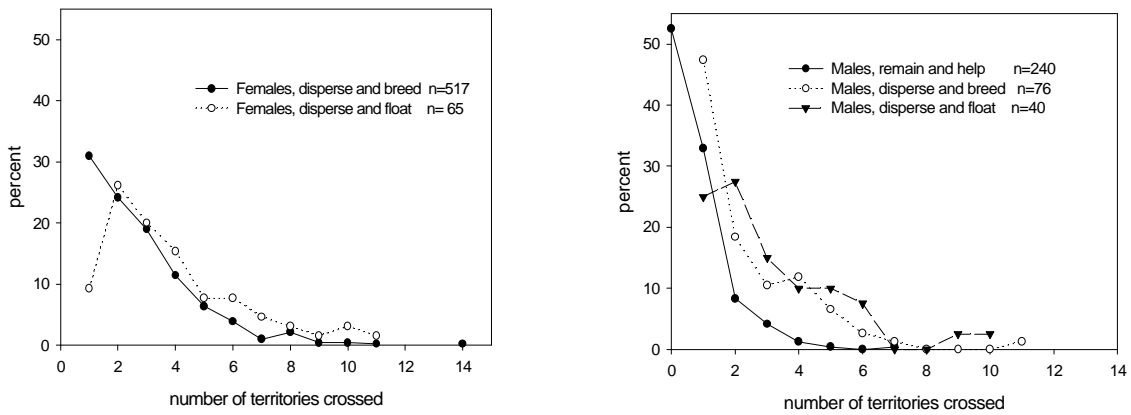

Figure 4.2. Distributions of natal dispersal distance of red-cockaded woodpeckers in number of territories crossed by life history as one year-olds.

SPATIAL DISTRIBUTION OF KIN

Closely related males were not randomly distributed throughout the territories within female dispersal range, but were clustered near the natal territory. For 109 one year-old breeding females in 1993, 1994, and 1995 combined, the proportion of closely related breeding males in the neighborhood of the breeding female was inversely correlated with the distance that the female dispersed (Figure 4.3; Spearman rank correlations; n=109; distance in km. and proportion of close kin: R=-0.34, p=0.0003; distance in territories and proportion of close kin: R=-0.27, p=0.004).

Figure 4.3. Boxplots of the proportion of closely related breeding males in the neighborhood of the breeding female (natal and breeding sites excluded), categorized by female dispersal distance in number of territories crossed. Boxplots indicate mean proportion, standard error, standard deviation, and outliers (>SE+1.5*2SE). There is a significant correlation (Spearman rank, n=109, R=-0.27, p=0.004).

Females with closely related mates dispersed significantly shorter distances than did females with unrelated mates for distance measured in kilometers (two-tailed median test, n=19,431, X^2=6.6, p=.01). For dispersal distance measured in territories crossed, the difference between females with closely related and unrelated mates was marginally significant (X^2=3.2, p=.07). Thus, increasing dispersal distance decreases the likelihood of close inbreeding because close kin are not randomly distributed throughout the territories within dispersal range.

In contrast, moderately related males were not clustered near the natal territory, but were scattered throughout the territories within female dispersal range. The proportion of moderately related males in the neighborhood in which the female bred was not correlated with the distance

that female dispersed (Figure 4.4; Spearman rank correlations, n=109, distance in km. and proportion of moderate kin: R=-0.13, p=0.16; distance in territories crossed and proportion of moderate kin: R=-0.05, p=0.58). In addition, dispersal distance of females with moderately related mates did not differ from that of females with unrelated mates (two-tailed median tests; n=53,431; territories crossed, X^2=0.5, p=0.83; kilometers, X^2=0.2, p=.66). Thus, decreasing dispersal distance does not increase the likelihood of mating with moderately related males, because these males are distributed throughout dispersal range.
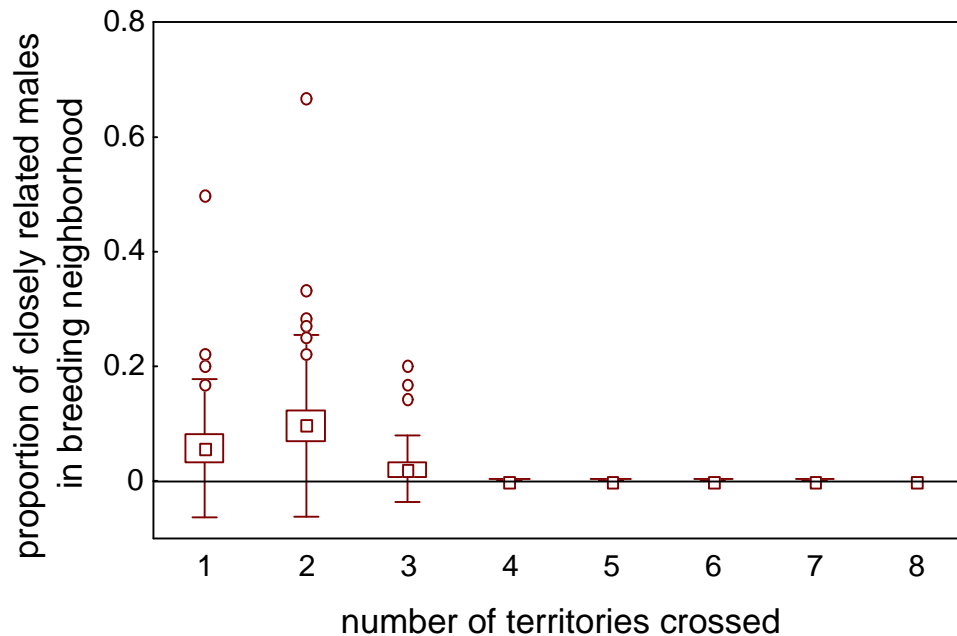

Figure 4.4. Boxplots of the proportion of moderately related breeding males in the neighborhood of the breeding female (natal and breeding sites excluded), categorized by female dispersal distance in number of territories crossed. Boxplots indicate mean proportion, standard error, standard deviation, and outliers. There is no correlation (Spearman rank, n=109, R=-0.05, p=0.58).

CHANGE IN THE FREQUENCY OF DISPERSAL FROM THE NATAL SITE

The frequency of dispersal from the natal territory was significantly different for females with and without a chance of inbreeding on that territory (Table 4.2). Females without a chance of inbreeding on the natal territory dispersed less frequently than expected, and females with a chance of inbreeding remained on their natal territory less frequently than expected. Inbreeding avoidance is therefore significantly associated with dispersal of females from their natal territory.

Table 4.2. Frequency of dispersal of female red-cockaded woodpeckers from the natal territory, with and without a chance of inbreeding on that territory. Expected values are given in parentheses.

	Female dispersed	Female did not disperse	X^2_c	p-value[1]
with chance of inbreeding	158 (153.5)	3 (7.5)	14.8	0.001
without chance of inbreeding	27 (31.5)	6 (1.5)		

[1]Chi-square test with continuity correction factor, df=1.

CHANGES IN NATAL DISPERSAL DISTANCE

There was no correlation between dispersal distance and the proportion of closely related males neighboring the natal site (Figure 4.5, Spearman rank correlations: n=109; proportion of close kin and territories crossed, R=-0.06, p=0.53; proportion of close kin and kilometers, R=-0.10, p=0.31). Similarly, there was no correlation between dispersal distance and the proportion of moderately related males neighboring the natal site (n=109; proportion of moderate kin and territories crossed, R=0.08, p=0.41; proportion of moderate kin and kilometers, R=-0.02, p=0.86). Thus, females do not disperse farther when closely related males are nearby, nor do they disperse shorter distances when moderately related males are nearby.
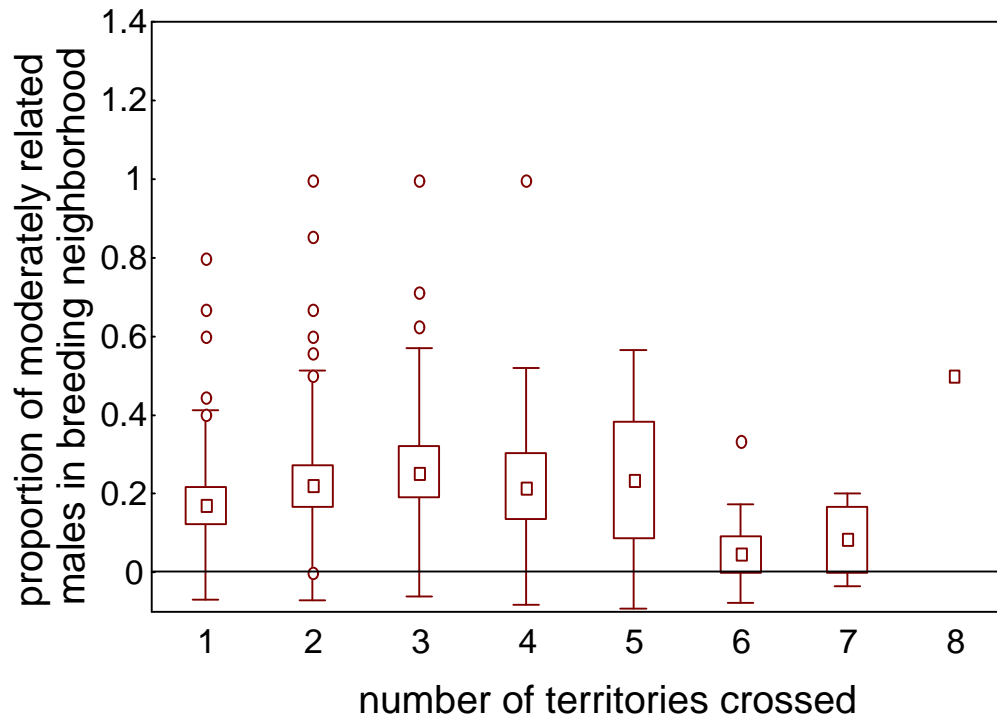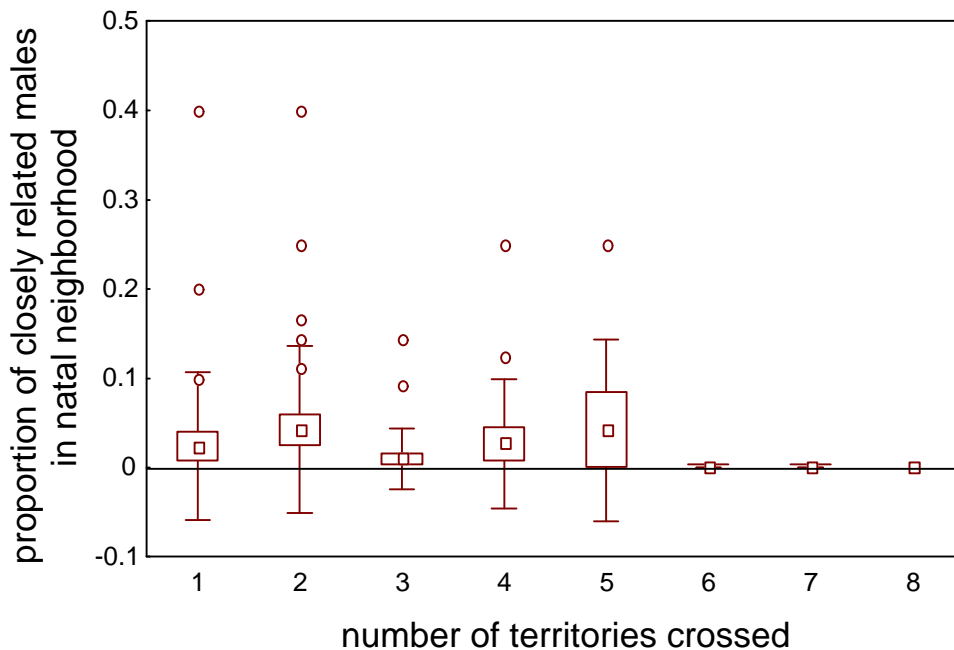

Figure 4.5. Boxplots of the proportion of closely related breeding males in the neighborhood of the female's natal territory (natal and breeding sites excluded), categorized by female dispersal distance in number of territories crossed. Boxplots indicate mean proportion, standard error, standard deviation, and outliers. There is no correlation (Spearman rank, n=109, R=-0.14, p=0.14).

Dispersal of young females is undoubtedly highly dependent on the breeding vacancies in the population. Females may change dispersal behavior in response to the kinship of breeding males occupying territories on which there are available vacancies. Because closely related mates are clustered near the natal territory (see above), inbreeding avoidance predicts that females with closely related mates on territories with vacancies will disperse farther than those without closely related mates on territories with vacancies. For 112 young females dispersing to these vacancies, there was no correlation between the number of closely related males on all territories with vacancies and the distance the female dispersed (Spearman rank correlations; n=112; number of close relatives and territories crossed, R=-0.14, p=0.14; number of close relatives and kilometers, R=-0.11, p=0.25). Therefore, I found no evidence that natal dispersal distance increases in the presence of closely related males, either near the natal site or on territories containing female vacancies.

I performed a similar test for change in female dispersal distance in response to the number of moderately related males on all territories with vacancies despite the evidence that males moderately related to a female are distributed throughout dispersal range (see above). There was no correlation between the number of moderately related males with vacancies and dispersal distance (Spearman rank; kilometers: R=0.04, p=0.72; territories: R=0.03, p=0.75). Therefore there is no evidence that natal dispersal distance decreases in the presence of moderated related mates, either near the natal site or on territories containing female vacancies.

KINSHIP AND THE FREQUENCY OF OCCUPYING THE CLOSEST VACANCY

The final tests for inbreeding avoidance and optimal inbreeding were comparisons of the frequency of one year-old females dispersing to the closest vacancy and the number of times there were closely and moderately related males in that vacancy. Kinship of males in the closest vacancy had no detected effect on whether or not the female occupied that vacancy, for either closely or moderately related males (Table 4.3).

Table 4.3. The number of times a one year-old dispersing red-cockaded female occupied the nearest vacancy, by the kinship of the male in that territory. Closely related males were those for which f>0.1; moderately related males were those for which 0<f<0.1. Expected values are given in parentheses.

	Did the female occupy the nearest vacancy?		X^2_c	p-value[1]
Was that male closely related?	Yes	No		
Yes	2 (2.5)	9 (8.5)	0.1	0.7
No	23 (22.5)	78 (78.5)		
Was that male moderately related?				
Yes	7 (6.9)	24 (24.1)	0.0	1.0
No	18 (18.1)	63 (62.9)		

[1]Chi-square test with continuity correction factor, df=1.

DISCUSSION

This study makes several important contributions to research into dispersal and kinship. First, it presents important evidence that inbreeding avoidance influences dispersal from the natal territory. Although the instances in which there is no chance of close inbreeding on the natal site are rare, dispersal of female fledglings in these cases is clearly reduced. Second, this study reveals no evidence that either inbreeding avoidance or optimal inbreeding influences dispersal distance, at least within the observed distance range. There is no facultative change in dispersal distance in the presence of moderately or closely related males, and dispersal distance of most females is not far enough to avoid close relatives. Selection against mating between close relatives has been demonstrated in this population (Chapter 3), but benefits of short-distance dispersal probably outweigh costs. The benefits of short-distance dispersal, however, do not appear to include optimal inbreeding, because moderately related males are distributed throughout female dispersal range.

A third contribution of the study is the methodology used to examine the effect of kinship on dispersal distance. Assessing kinship of the males neighboring the breeding female provides insight into the distribution of relatives, while assessing kinship of males neighboring the natal territory may reveal differences in dispersal behavior in the presence of relatives. Few previous studies of wild populations have attempted to detect changes in dispersal in the presence and absence of kin, and none have distinguished moderate and close relationships. The analyses used here are not without problems, however. For example, the use of larger or smaller neighborhoods may have yielded different results. In addition, analyses were confined to the observed range of dispersal distances, and therefore there was little investigation into constraints on dispersal distance.

NATAL DISPERSAL IN RED-COCKADED WOODPECKERS

This study describes the natal dispersal of red-cockaded woodpeckers in south-central North Carolina. Dispersal distances are comparable to those reported for other cooperative breeders: for all females, distances ranged from 0-14 territories with a mean and median of 2.8 and 2 territories respectively; for all males, distances ranged from 0-11 territories with a mean and median of 1.3 and 1 territories respectively. In splendid fairy wrens (*Malurus splendens*), females and males disperse a median of 1 and 0 territories with a range of 0-11 (Russell and Rowley 1993). Female Florida scrub jays (*Aphelecoma caerulescens*) disperse a mean of 3.44 and a median of 2 territories, while males disperse a mean of 0.9 and a median of 0 territories (Woolfenden and Fitzpatrick 1984). Short-distance dispersal, in addition to delayed dispersal, is characteristic of cooperative breeders (Zack 1990).

Dispersal in this population of woodpeckers, like that of several other cooperative breeders, is clearly sex-biased: females disperse farther than males, and females that float or disperse and breed as one year-olds disperse farther than males exhibiting these same life histories. Splendid fairy-wrens exhibit an overall sex bias in dispersal because males inherit the natal territory more often than females, but dispersing females and dispersing males travel equal distances (Russell and Rowley 1993). Dispersal in Florida scrub jays is sex-biased; most males

acquire a portion of the natal territory while females generally do not, but moreover, dispersing females travel farther than dispersing males (Woolfenden and Fitzpatrick 1984).

Non-cooperatively breeding birds in general disperse farther distances (Zack 1990) and may exhibit sex-biased dispersal less often than cooperatively breeding birds. Median dispersal distance of song sparrows (*Melospiza melodia*) on Mandarte Island varied annually from 8 to 21 territories (Arcese 1989), distances substantially greater than those given above for cooperative breeders; no sex bias in distance of song sparrows was found (Arcese 1989). Dispersal distance for indigo buntings (*Passerina cyanea*) returning to their natal population as yearlings was generally less than 2 kilometers. However, only 5.4% of fledglings returned (Payne 1991). Neither return rates nor dispersal distances of returning indigo buntings differed significantly between males and females (Payne 1991). While other non-cooperative birds do exhibit sex bias in dispersal (reviewed by Greenwood 1980), it is clear that sex-biased dispersal is "particularly pronounced" in group-living birds (Pusey 1987).

CHANGE IN THE FREQUENCY OF DISPERSAL FROM THE NATAL SITE

Dispersal of females from their natal site decreases if there is no chance of close inbreeding. In almost 20 percent (6 of 33) of sites with an opening for a breeding female but without a closely related breeding male, female fledglings stayed to breed in the following year, whereas less than 2 percent (3 of 161) of female fledglings remain at home to breed with a close relative. The exact timing of death or dispersal is unknown, so some females may disperse prior to the death of their mother or father. Even so, the data reveal a significant effect of close relatives. This change in dispersal rates in the absence of close relatives in combination with the documented costs of close inbreeding (Chapter 3) clearly shows that inbreeding avoidance affects dispersal of female fledglings. Inbreeding avoidance may not be the only factor affecting dispersal from the natal site, but it is certainly one factor.

Kin recognition based on familiarity (i.e. association, reviewed by Holmes and Sherman 1983) is undoubtedly the mechanism underlying the ability of fledgling females to change their dispersal behavior based on the presence or absence of male relatives on the natal territory. Kin recognition through familiarity is also evidenced in this species by changes in the dispersal behavior of breeding females. Among females experiencing the death of their mates, kinship of the new breeding males is an extremely important factor in determining whether or not females disperse from breeding sites (Walters et al. 1988, Chapter 2). Kin recognition by breeding females is more sophisticated than simple familiarity, however: females with familiar but unrelated males as potential new mates did not disperse as frequently as those with familiar, related males (Chapter 2). It is not possible to test for a similar ability in fledgling females to distinguish close kin from among familiar males.

Similar change in dispersal behavior in the presence of kin has been documented for the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*): individuals do not disperse from the natal site when there is no chance of close inbreeding (Koenig and Pitelka 1979, Hannon et al. 1985).

INBREEDING AVOIDANCE AND DISPERSAL DISTANCE

For dispersal distance to be influenced by inbreeding avoidance, close inbreeding must be costly and increased distance must lower the likelihood of inbreeding. Significant reproductive costs of close inbreeding have been documented in this population (Chapter 3), and both the frequency of closely related pairs and the number of closely related males in the breeding female's neighborhood decrease with increasing female dispersal distance.

There was, however, no change in dispersal behavior in the presence of closely related males near, but not on, the natal territory. Two analyses failed to show the predicted change in dispersal behavior: natal dispersal distance did not change between those females with one or more closely related males neighboring the natal territory and those with no close relatives nearby, and natal dispersal distance did not change between females with and without close kin on territories with available vacancies. Additionally, the number of young females occupying the vacancy nearest the natal territory was unaffected by whether or not that breeding male was closely related.

Among other species of birds, spatial distribution of close kin varies considerably. Chances of inbreeding among great tits in Wytham Wood decreased with increasing dispersal distance (Greenwood et al. 1978). However, a more detailed study of dispersal and kinship of great tits in Vlieland described an even distribution of relatives throughout the largest sub-population (van Tierenden and van Noordwijk 1988) Similarly, the probability of mating with kin was independent of dispersal distance for song sparrows (*Melodia melospiza*) on Mandarte Island (Arcese 1989).

Ability to discern kin varies considerably among species as well. Acorn woodpeckers recognize close kin on the natal site, as evidenced by corresponding change in dispersal behavior. In contrast, indigo buntings showed no ability to distinguish close kin: the return of opposite-sex parents or siblings in this migratory species had no effect on dispersal distance (Payne 1991). Similarly, neither great tits (van Tierenden and van Noordwijk 1988) nor Darwin's medium ground finches (*Geospiza fortis*, Gibbs and Grant 1989) show evidence of active kin recognition or avoidance of closely related mates.

The predictable spatial distribution of closely related males in a red-cockaded woodpecker population (that is, clustered near the natal territory,) is more conducive to selection for dispersal distances that serve to avoid inbreeding than the random distribution of kin in many non-cooperative species. Additionally, the documented cost of close inbreeding in this population is evidence that selection against inbreeding is in place. Surprisingly, though, most females do not disperse far enough to avoid close relatives. The modal dispersal distance for females is one territory (Figure 4.1), and the median distance is two territories (Table 4.1). In light of the evidence that females do not change distance in the presence of relatives, modal and median distance would have to be four territories or more if distance served to avoid closely related males (Figure 4.4).

Thus, selection against close inbreeding has not been strong enough to promote longer distances. The likelihood of mating with close kin may be so low, even for those that disperse

only one territory, that inbreeding costs become insignificant. For females dispersing fewer than four territories, the proportion of closely related males within the natal neighborhood is lower than 0.1, (Figure 4.3), or less than one out of ten. Additionally, selection for shorter dispersal distances may outweigh or be balanced by selection against close inbreeding.

OPTIMAL INBREEDING AND DISPERSAL DISTANCE

For dispersal distance to be influenced by optimal inbreeding, moderately related pairs must show reproductive benefits and the likelihood of mating with moderate kin must change with distance. For this species, the benefits of moderate inbreeding are ambiguous and do not appear to be under selection (Chapter 3), and no relationship between dispersal distance and the distribution of moderately related males was found. Females with moderately related mates dispersed equal distances as those with unrelated mates, and the number of moderately related males neighboring breeding females did not change with female dispersal distance. Additionally, dispersal distance did not change with the presence of moderate kin near the natal territory, and the number of females occupying nearest vacancies was unaffected by the presence of a moderately related male in that site.

Thus, I found no evidence that optimal inbreeding affects natal dispersal distance. There is no evidence of an active mechanism to recognize moderate kin, and no pattern in the distribution of moderate kin within the range of dispersal distances. However, my analyses tested for an effect of optimal inbreeding within dispersal range only. The spatial distribution of moderate kin may change beyond this dispersal range, and optimal inbreeding may yet prove to be a significant factor in determining the distribution of dispersal distances in this species. Further research is necessary to identify the role of optimal inbreeding at a larger spatial scale.

Preference for moderately related mates in other wild populations of birds is virtually unexplored, with one notable exception: kinship of great tits did not differ between pairs and the closest neighbor of the opposite sex (van Tierenden and van Noordwijk, 1988). This was a test, similar to those in this study, of females actively choosing related mates within dispersal range. The possibility that dispersal distances may themselves be limited by costs of outbreeding was not addressed.

POSSIBLE FACTORS PROMOTING SHORT-DISTANCE FEMALE DISPERSAL

Females in this population disperse surprisingly short distances, most often only one or two territories. Benefits of short-distance dispersal must overwhelm the documented costs of close inbreeding. Such benefits may include a competitive advantage to nearby females in attempts to attain breeding positions.

Studies of the delayed dispersal exhibited by males of this species, and of cooperative breeding in general, have attributed this social system to unusually high variation in territory quality (Koenig et al. 1992, Walters et al. 1992). High variation in territory quality increases competition for breeding vacancies in high-quality habitat. Such intense competition promotes delayed dispersal, because individuals born into good territories can gain fitness by remaining on

the natal territory, despite postponing reproduction, in exchange for a breeding position in a high-quality territory (Koenig et al. 1992, Walters et al. 1992).

I suggest that, although only male red-cockaded woodpeckers do exhibit delayed dispersal, intense competition for breeding vacancies is affecting female dispersal as well. Thus, females may occupy breeding positions in nearby territories because such positions are easier to obtain. Such an advantage to nearby females could result from prior knowledge of a vacancy, if females assess vacant/occupied status of territories within a given search range.

The risk of mating with a close relative and its associated inbreeding depression may be less than the risk of not obtaining a breeding vacancy if dispersal distance is increased. However, the risk of close inbreeding may increase with decreasing population size. Whether dispersal behavior differs with increasing risk of close inbreeding is an interesting question requiring further research.

CHAPTER 5: SUMMARY

Here, I give summaries of my research into the dispersal of female red-cockaded woodpeckers. Each of the following sections summarizes a corresponding chapter.

BREEDING DISPERSAL

I tested four hypotheses for the cause of between-season dispersal of breeding female red-cockaded woodpeckers within a large population: inbreeding avoidance, mate choice, site choice, and social constraints. I also investigated the effect of the age of the female on dispersal behavior, and analyzed relationships among rates of dispersal, site-fidelity, and mortality.

Breeding dispersal in this species has multiple causes. Breeding females disperse to avoid inbreeding (inbreeding avoidance) and to attain a higher-quality mate (mate choice). Inbreeding avoidance was illustrated by 45 movements of breeding females out of 49 cases in which the female's son attained breeding status in the female's territory. Close inbreeding in this species causes loss of fitness (Chapter 3). Mate choice was evidenced by increased dispersal rates among females that, after suffering the death of their mates, faced breeding with young replacement males. Breeding with young males had fitness costs: young males had increased rates of nest failure and decreased numbers of nest attempts.

Tests for dispersal to improve site quality (site choice) gave ambiguous results. Dispersal decreased with the presence of helpers on the original territory, a sign of high territory quality, and dispersal was associated with reproductive failure among young females. However, analyses using an index of territory quality based on site-specific mortality and reproduction failed to provide evidence that dispersing females improved site quality.

Breeding females do not appear to disperse in response to social constraints, including within-group resource competition, reproductive competition between females and helper sons, and female-female competition for breeding vacancies. Resource competition and reproductive competition were not supported because breeding dispersal did not increase with the presence of helpers on the original territory. Female-female competition was not supported because dispersing females were older than the females replacing them both as a group and in 58 of 65 dispersal events in which both ages are known exactly. Replacement females are dominant to dispersing females only if dominance is not associated with age.

Young females are more likely to disperse than older females. Females two years of age and younger are more susceptible to reproductive failure than older birds, but also are more likely to disperse in response to reproductive failure than are older birds.

Breeding dispersal in this species does not appear to be driven by mortality rates, because annual variation in dispersal does not vary with that of mortality. However, rates of mortality and dispersal both increase under certain circumstances, such as a female's son attaining breeding

status in her territory. This correlation of dispersal and mortality by circumstance was used to suggest the cost of breeding dispersal for this population.

COSTS, BENEFITS, AND FREQUENCY OF INBREEDING

I assessed the costs, benefits, and frequency of inbreeding in a large population of red-cockaded woodpeckers in south-central North Carolina. Analysis of eight fitness variables revealed significant fitness costs of close inbreeding. Close inbreeding had two separate effects on fitness. Closely related pairs (sample size from 21 to 26, kinship coefficient greater than 0.1) had significantly lower hatching rates than unrelated pairs (sample size from 725 to 767, kinship coefficient equal to 0.0), which translated into fewer nestlings, fledglings, and yearlings; closely related pairs also exhibited a marginally significant reduction in fledgling survival. Moderately related pairs (sample size from 57 to 70, kinship coefficient between 0.0 and 0.1) exhibited significantly higher hatching rates than unrelated pairs, but this effect did not result in more yearlings produced. Recruitment of female fledglings into the breeding population was significantly associated with their level of inbreeding: both highly inbred females and moderately inbred females became breeders fewer times than expected.

The effect of inbreeding on the reproduction of individuals was remarkably similar to that exhibited in the reproduction of pairs. Highly inbred individuals (sexes pooled, sample size from 6 to 8) showed a marginally significant reduction in hatching rates and significantly fewer nestlings per year than non-inbred individuals. Moderately inbred individuals (sexes pooled, sample from 19 to 34) exhibited a significant increase in hatching rates.

The frequency of observed inbreeding in this population was compared to an expected frequency derived from 50 rounds of random pairing of individuals. This comparison was repeated for three spatial scales: the entire study area, four regions within the study area, and small artificially designated neighborhoods within one region of the study area. Mating within this population is not random: observed inbreeding was higher than expected based on random mating for the entire study area; higher than expected for three of four regions; and lower than expected among neighborhoods. A severe drawback to this technique is that it identifies pattern, not process; it cannot distinguish between possible causes of non-random mating, such as dispersal distance and behavioral avoidance or preference of relatives as mates.

NATAL DISPERSAL AND INBREEDING

I investigated the potential effects of inbreeding avoidance and optimal inbreeding on the natal dispersal of female red-cockaded woodpeckers within a large population in south-central North Carolina. I compared the spatial distribution of closely and moderately related males with dispersal distances of females, to reveal whether these distances served to avoid close inbreeding and/or promote moderate inbreeding. I then assessed the potential change in dispersal behavior of females in the presence or absence of close and moderate kin.

Closely related males were predictably distributed in space—they were clustered near the female's natal territory. However, the dispersal distance of most females was not sufficient to avoid closely related males as mates. Females would have had to move three or more territories to avoid all closely related males, but median and modal dispersal distance was two and one territories, respectively. Moderate kin were not clustered near the natal territory, but were found throughout the range of female dispersal distance.

Females changed dispersal behavior in the presence of close kin on the natal site—clear evidence of inbreeding avoidance. Although females almost always dispersed from their natal site, they dispersed less frequently if there was no chance of close inbreeding there in the following year. Females did not change dispersal behavior in the presence of close or moderate kin that are not on the natal site. Dispersal distance did not increase with increasing numbers of closely related males near (but not on) the natal site, nor did dispersal distance decrease with increasing numbers of moderately related males near the natal site. In addition, the frequency of dispersal to the nearest territory with breeding female vacancy was unaffected by the kinship of the breeding male holding that territory. Females did not avoid the nearest vacancy if there was a closely related breeding male there, nor did they disperse there more frequently if there was a moderately related male there.

Inbreeding avoidance affects dispersal from the natal site, but does not affect dispersal once females have left the natal site. Unknown benefits of short-distance dispersal must overwhelm the documented cost of close inbreeding. One such benefit may be that nearby females have an advantage when competing for breeding vacancies. Optimal inbreeding does not influence natal dispersal within the observed range of female dispersal distances. While it may yet prove to be a factor influencing maximum distance, it is not promoting the extremely short dispersal distances documented here.

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APPENDIX A

Descriptive statistics for the territory quality index and its components, n=327.

component	mean	std	median	range
quality (TQ)	3.47	2.62	2.97	0.00-14.00
no. fledglings/years	0.99	0.60	1.00	0.00-2.86
no. dead/bird-years	0.36	0.17	0.32	0.06-1.00
no. fledglings	13.88	8.72	14	0-39
no. dead	7.16	3.82	7	1-17
bird-years	22.70	11.82	24	1-52
years	14.18	3.13	15	1-16

curriculum vitae

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